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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

A MULTISCALE ANALYSIS OF NEST-SITE CHOICE, NEST SUCCESS, AND POPULATION ABUNDANCE IN THE SCISSOR-TAILED FLYCATCHER (*TYRANNUS FORFICATUS*)

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

David L. Certain
Norman, Oklahoma
2000

A MULTISCALE ANALYSIS OF NEST-SITE CHOICE, NEST SUCCESS, AND POPULATION ABUNDANCE IN THE SCISSOR-TAILED FLYCATCHER (*TYRANNUS FORFICATUS*)

A Dissertation approved for the

DEPARTMENT OF ZOOLOGY

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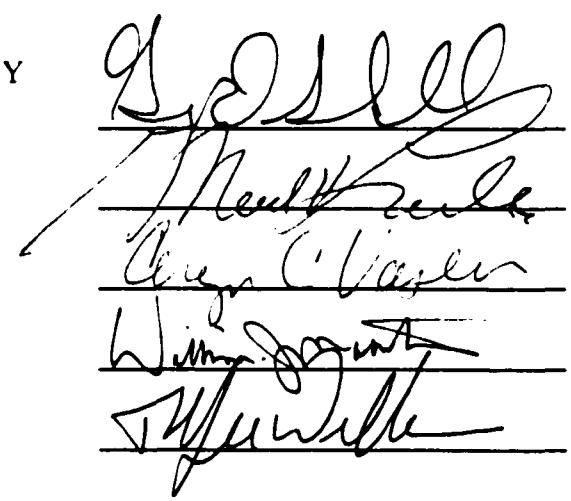

PREFACE

This dissertation is presented as three chapters. Each chapter has been submitted to a refereed journal and is formatted accordingly. The first chapter has been submitted to *Wilson Bulletin*, and the second and third chapters to *Oecologia*.

ABSTRACT

Large-scale declines in the abundance of many bird species in North America has led to increased research on the nesting habits of these species. Nest-site choice by birds can significantly affect the probability of successful reproduction and can occur at scales ranging from the area immediately surrounding the nest to that of the multi-patch landscape across which a population is distributed. In addition, characteristics of landscape structure (e.g. fragmentation) may influence local abundance, resulting in geographic-scale avian abundance patterns. I measured structural and compositional characteristics of habitats on the Fort Sill Military Reservation in southwest Oklahoma and along Breeding Bird Survey (BBS) routes across the geographic range of the scissor-tailed flycatcher (*Tyrannus forficatus*) to examine associations between nest-site choice, nest success, and the distribution patterns of local abundance.

Results showed that scissor-tailed flycatchers used structural and compositional characteristics at multiple scales to select nest sites on Fort Sill. Many of the characteristics selected would tend to conceal and isolate nests from potential nest predators. Successful nest sites had less woody edge and tended to be further away from the nearest woody edge than depredated nests.

I used BBS data and habitat maps to examine associations of landscape structure and composition with the relative mean abundance of the scissor-tailed flycatcher. Routes were scattered over most of the breeding range. Landscape variables were significantly associated with abundance. Relative abundance and landscape variables exhibited spatial autocorrelation. However, differences in landscape variables remained

significantly associated with differences in abundance after allowing for spatial structure.

These findings show that structural and compositional characteristics of habitat at multiple scales surrounding nest sites can have a significant influence on habitat choice and fitness in birds. These data also support previous findings that edge habitats have negative effects on reproductive success of breeding birds and indicate that birds nesting in prairie habitats face some of the same selective pressures as those nesting in fragmented forest landscapes. Finally, results suggest that landscape structure influences local avian abundance and range-wide abundance patterns, most likely via influence on local reproductive success.

ACKNOWLEDGMENTS

I thank my major advisor, Dr. Gary D. Schnell, for all of his efforts to teach and train me to be a thoughtful, professional, well-rounded ecologist. I am also grateful to advisory committee members Drs. Mark V. Lomolino, William J. Matthews, Caryn C. Vaughn, and T. H. Lee Williams for their input and encouragement throughout this endeavor.

Thanks to Linda Bird, Jason Cook, Chuck Dillon, David Garcia, Raniyah Ramadan, Jane Sund, Bill Vieux, John Ware, and Brad Watkins for their assistance in the field and in the laboratory during the many hours of digitizing aerial photographs. Generous and appreciated financial support for this work was provided by: U.S. Department of Defense, U.S. Army Research Office, and Office of Naval Research (AASERT No. DAAH04-93-G-0093); Department of Zoology, University of Oklahoma; Oklahoma Biological Survey; and George Miksch Sutton Scholarships in Ornithology.

My deepest personal thanks to the many faculty, staff, and students associated with the Department of Zoology and the Oklahoma Biological Survey who made my many years here an experience I will never forget. A special thanks to Wendy, Nancy, and Terry Anderson for providing the family support that I needed when my own family could not be there. Finally, I thank my parents, Charles E. Certain and Sherian G. Brumley, and the rest of my family for their constant encouragement and understanding.

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NEST-SITE SELECTION AND NEST SUCCESS OF SCISSOR-TAILED FLYCATCHERS IN SOUTHWESTERN OKLAHOMA

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ABSTRACT.—Nest predation is the leading cause of nest loss in birds and has been important in the evolution of avian life-history strategies. We investigated the relative importance of nest concealment and isolation in nest-site selection and nest success for Scissor-tailed Flycatchers (*Tyrannus forficatus*) in southwestern Oklahoma. Nest concealment and isolation both within the nest tree and the area surrounding the nest tree were measured to investigate effects of scale. Scissor-tailed Flycatchers suffered significant nest losses during three seasons (1994-1996). The Mayfield estimate of the probability of nest success was 0.36 across all three seasons. Predation by unknown predators was indicated in 81% of all nest losses. Nest sites typically were in taller trees with a higher and less-variable density of woody stems at or near nest height. The areas surrounding nests were also less variable than expected by chance in the amount of woody, forb, and rocky ground cover. A discriminant function based on a set of composite variables correctly classified 72% of all sites as being a nest site or a non-nest site. The discriminant model classified nest and non-nest sites based on woody vegetation height, number of trees, and amount of rocky and woody ground cover near the nest. Successful nest sites showed significantly less variation in the distance from the main stem of the nest tree to the nest when compared to unsuccessful nest sites. Overall classification accuracy of successful and unsuccessful nests by a discriminant function was marginal, with 66% of nests being correctly classified. Nest sites were classified based on the amount of rocky ground cover near nests. These results generally supported the supposition that nest sites are selected for both concealment and isolation. Scissor-tailed Flycatchers also appeared to use characteristics of both the nest

tree and the area immediately surrounding the nest tree to select nest sites. *Received 2000, accepted*.

Predation is the primary cause of nest failure in breeding birds (Ricklefs 1969, Martin 1995) and may have a significant influence on the evolution of a variety of life-history traits, including timing of nesting, clutch size, and nesting period (Martin 1995). If nest predation significantly influences fitness, then natural selection should favor the selection of nest sites that reduce the risk of predation and increase the probability of nest success in areas where nest predation is common. One commonly cited hypothesis is that better-concealed nests are less likely to be discovered and preyed on by predators, and present a better chance for successfully fledging young. Numerous studies have provided evidence for the nest-concealment hypothesis by demonstrating significant positive effects of nest concealment on nest-site selection and nest success (e.g., Murphy 1983, Martin and Roper 1988, Kelly 1993, Norment 1993, Nolte and Fulbright 1996).

One alternative but non-exclusive hypothesis is that birds may select nest sites that are isolated from potential predators and that the relative importance of concealment and isolation may depend on the types of nest predators present in the environment (Clark and Nudds 1991). Nest concealment should be more important when avian or other visual predators are the primary causes of nest loss (Sugden and Beyersbergen 1986, 1987). Alternatively, nests in isolated or inaccessible positions should be selected and are more likely to succeed if predators using olfactory cues, as is

the case with nocturnal mammals and snakes, are dominant. Some combination of concealment and isolation of nests may be best when all of these predator types are present.

Nest predation is a significant cause of egg loss and nest failure for Scissor-tailed Flycatchers (*Tyrannus forficatus*) in southwestern Oklahoma (Regosin and Pruett-Jones 1995) and other parts of its range (Nolte and Fulbright 1996). The Scissor-tailed Flycatcher is a Neotropical migrant that breeds primarily in open country throughout Texas, Oklahoma, and Kansas and parts of New Mexico, Colorado, Nebraska, Missouri, Arkansas, and Louisiana (AOU 1998). Breeding individuals range over relatively large territories (> 1 ha) to forage and protect nest sites (Fitch 1950; Certain, pers. obs.).

Scissor-tailed Flycatchers possess characteristics that make them good candidates for studies of the effect of nest predation on nest success. Under otherwise similar environmental conditions, species with longer nesting periods should have greater exposure to potential nest predators. On Fort Sill, clutches of Scissor-tailed Flycatchers begin to appear during the first half of May, with a median clutch-initiation date late in the same month (Regosin and Pruett-Jones 1995). Their average nesting period (time from initiation of egg-laying to fledging of young) is relatively long, being more than 30 days (Fitch 1950, Regosin and Pruett-Jones 1995). In addition, Scissor-tailed Flycatchers often feed and nest in complex, naturally fragmented habitats, where the potential for nest predation may be substantial due to the abundance and diversity of potential predators associated with edge habitats (Robbins 1980, Whitcomb 1981, Wilcove 1985, Andren 1992, Marini et al. 1995).

In this study we investigated the importance of nest concealment and isolation as they relate to nest-site selection and nest success. We predicted that Scissor-tailed Flycatchers in southwestern Oklahoma would choose nest sites that were more concealed and isolated from potential predators than a random selection of potential nest sites, and that successful nests would be more concealed and isolated than unsuccessful nests.

METHODS

Study area.—Our study was conducted on the Fort Sill Military Reservation, Comanche County, in southwestern Oklahoma. Fort Sill encompasses an area of 38,000 ha of primarily short- and mixed-grass prairie habitats. Other land-cover types found on Fort Sill include tallgrass prairie, rangeland, agriculture, mesquite savanna, oak savanna, riparian woodland, cross timbers, bottomland forest, and urban (Pogue 1998).

Nest sampling.—We monitored nesting attempts by Scissor-tailed Flycatchers between early May and late July of 1994-1996. The sampling area was searched both by driving roads and walking through roadless areas. Nests were located by searching trees and shrubs or by following adults until they returned to a nest site. Areas that were off-limits on the military reservation (e.g., live-fire zones) or that could not be accessed on a regular basis were excluded from the sampling region. Some land-cover types were not extensively sampled because they represented habitat types not typically used by Scissor-tailed Flycatchers (e.g., cross-timbers, bottomland); however, we sampled edge habitats involving these land-cover types. Given the degree of human activity, we

also excluded from analyses nest sites in the core of the cantonment area (i.e., area with housing and other buildings), where developed and landscaped areas were the dominant land-cover types. As a result of these exclusions, the actual sampling area included about one-third of the total area of Fort Sill (ca. 12,600 ha) and included all of the most extensive land-cover types found there.

At the time each nest was found, the number of eggs or nestlings was recorded, and nests were revisited every 2-8 days ($\bar{x}$ = 3.6) until the outcome of the nesting attempt was determined. Nest contents seldom were touched. Nests were considered to be successful if at least one chick fledged. Nest loss was attributed to predation if the nest was generally intact in the nest tree and all eggs or chicks were missing. Loss due to extreme weather was typically indicated when eggs, chicks, or the entire nest was found on the ground after a known storm event. Deserted nests were indicated by the lack of adults at or near the nest during at least two monitoring visits; often eggs were addled or chicks were dead. In these cases, the proximate cause of mortality could have been either starvation or excessive heat. All other instances of nest loss were attributed to unknown causes.

Nest success was calculated for each breeding season using the Mayfield (1961, 1975) method, which allowed us to estimate a daily survival probability during the incubation and nestling periods, as well as an overall probability of nest success. Individual birds were not marked, so we were unable to confirm multiple nesting attempts by the same pair. This could result in some bias in estimates of nest success for individual pairs, but should not unduly affect populationwide estimates.

Vegetation sampling.—Because habitat characteristics important to nest concealment exist at multiple scales (Martin and Roper 1988, Bergin 1992, Kelly 1993, Norment 1993, Nolte and Fulbright 1996), we measured a total of 27 variables that described nest placement, nest cover, and vertical and horizontal vegetation structure at the scale of the nest tree, as well as at a scale that included an area surrounding each nest tree (Table 1). Variables measured follow those described by Murphy (1983) and James and Shugart (1970) with some modifications.

We measured the height of each nest and nest tree and calculated the ratio of nest height to tree height (relative nest height). We also recorded the distance from the main, central stem of the nest tree to the edge of the canopy along a horizontal axis running through the nest. Along the same axis we noted the distance from the main stem to the center of the nest. We calculated the ratio of distance to nest to distance to canopy edge to determine the relative distance of the nest from the main stem. We evaluated the degree of cover immediately surrounding the nest by estimating the amount of cover in each of the four cardinal directions and directly above the nest within an imaginary sphere extending 10 cm from the edge of the nest. Cover in each direction was classified by the amount of space occupied by vegetation: (1) 0-25% occupied, (2) 26-50%, (3) 51-75%, and (4) 76-100%. The mean of these five numbers was used as the final estimate.

Other concealment and isolation estimates were made by measuring vegetation characteristics within a 0.04-ha circular plot (11.25-m radius) centered on the nest tree. We created two orthogonal axes on the ground using measuring tapes, with each axis

centered on the nest tree. The direction of the first axis direction was randomly chosen. Measures within this sample plot and along the axes described vertical and horizontal vegetation patterns of the nest tree and vegetation surrounding the tree. The total number of trees ≥7.6 cm in diameter at breast height (dbh) were counted within each plot. The number of quadrants with trees ≥7.6 cm dbh present was used as an index of tree distribution around the nest tree. We assumed that nest concealment increased with the number of quadrants occupied by other trees. We also counted the number of woody stems that made contact (hits) with a range pole extending vertically into the canopy. Total stem hits were counted for the following 11 height intervals (in meters): 0.0-0.5, >0.5-1.0, >1.0-1.5, >1.5-2.0, >2.0-2.5, >2.5-3.0, >3.0-3.5, >3.5-4.5, >4.5-5.5, >5.5-6.5, and >6.5-7.5. Counts were made at 2-m intervals along each orthogonal axis, and hits were summed for each height interval. This was an estimate of vegetation density that included the nest-tree canopy and the canopy of trees and shrubs surrounding the nest tree. We also measured canopy height along each axis and calculated mean canopy height. Finally, we determined percent ground cover along each axis for six ground cover types: woody vegetation, forbs, grass, leaves, rock, and bare ground.

To test for evidence of habitat selection we measured all of the above vegetation characteristics not related to nest placement at a group of non-nest sites, each centered on a tree where there was no active Scissor-tailed Flycatcher nest present. Non-nest sites were chosen from among sites being used in an on-going project to inventory and monitor natural resources on Fort Sill (Land Condition Trend Analysis [LCTA]; Tazik

et al. 1992). The distributions of LCTA sites and our non-nest sites were stratified-random such that sites were proportionally representative of the major land cover types included in our sampling area. Selecting non-nest sites in this way could lead to an overestimate of variance for variables at non-nest sites, thereby increasing the likelihood of a statistically significant result and evidence of nest-site selection. However, exploratory data analysis showed that variance at nest sites was just as likely as non-nest sites to be significantly larger.

Statistical analyses.—We used a row-by-column *G*-test of independence with Williams' correction to examine differences in the frequency of successful and unsuccessful nests among years (Sokal and Rohlf 1995). We employed *t*-tests with Bonferroni adjustments to account for multiple comparisons (Hays 1994), and tests for homogeneity of variance to examine habitat differences between nest sites and non-nest sites, as well as between successful and unsuccessful nests. Tests for differences in mean and variance can provide information about nest-site selection that tests of means alone cannot (Ratti et al. 1984, Nolte and Fulbright 1996). We considered nest-site selection to have occurred when: (1) group means were significantly different; (2) variance was significantly less at nest sites than non-nest sites; or (3) when group means were significantly different and variance was less at nest sites (Nolte and Fulbright 1996). Class variables were tested using the nonparametric Kruskal-Wallis test (Sokal and Rohlf 1995). Some types of variables better meet assumptions of parametric tests when transformed. As suggested by Sokal and Rohlf (1995), percent and ratio variables were arc-sine transformed. The values for the total number of trees in the sampling area

were transformed by multiplying raw values by the logarithm to base 10. We transformed the number of woody stems at each height interval by adding 1.0 to each value (to account for zero values) and calculating the square root.

Because results from previous studies of nest-site selection have shown that combinations of habitat variables often contribute strongly to differences between nest sites and random sites, as well as between successful and unsuccessful nests (Colwell 1992, Norment 1993), we employed *a priori* discriminant-function analysis (DFA) to look for linear combinations of variables that maximally discriminated between each pair of groups (McLachlan 1992). To account for correlations among variables, we first developed a new set of uncorrelated variables using principal components analysis (PCA). Major trends in the original variables were represented on principal components calculated from a correlation matrix calculated from standardized data (variable means of 0.0 and standard deviations of 1.0). We kept all resulting principal components with eigenvalues equal to or greater than 1.0. Component scores were based on standardized data and were used as input values for the DFA.

We used a forward-stepping approach in the DFA to determine the combination of standardized variables that best discriminated between groups. The F-to-enter in the classification function was set to 4.0, while the F-to-remove was 3.9. The accuracy of each model at discriminating between groups was based on a jackknifed classification procedure that effectively eliminated the site being considered, recalculated the discriminant function, and then classified the site based on the new coefficients. This approach typically gives a more conservative estimate of the accuracy of the function to

correctly classify sites (Schnell et al. 1986). All statistical tests, except for the *G*-test and tests for homogeneity of variance, were done using SYSTAT statistical software (version 7.0.1; SPSS, Inc. 1997). All other analyses were performed using BIOMstat (version 3.2; Applied Biostatistics, Inc. 1996).

Scissor-tailed Flycatchers may renest within the same territory both within and between years (Regosin and Pruett-Jones 1995). This behavior likely reduced the independence of some observations since we were unable to recognize individuals and track their nesting attempts. We increased statistical independence within our data set by eliminating from all analyses nests in nest trees in 1995 and 1996 that had been used in one or both previous years. Nest sites where nests were lost or where nest-area vegetation was significantly changed before we could measure vegetation parameters also were excluded from analyses. Unless otherwise stated, mean values and standard deviations are reported.

RESULTS

Nest success and predation.—Of 130 nesting attempts monitored from 1994-1996, at least one chick fledged from 45 nests (34.6%; Table 2). The probabilities of nest success as determined by the Mayfield method were 0.33, 0.38, and 0.37 for 1994-1996, respectively (0.36 overall). There was no difference in the relative frequency of successful and unsuccessful nests among years ($G = 0.77$, df = 2, $P = 0.68$). Of the 85 nest failures, 69 were attributed to nest predation, 5 to effects of weather, 6 to desertion, and 5 to unknown causes. Nest predation was the primary cause of nest loss during all

years.

Nest-placement statistics.—Table 3 summarizes values for nest-placement variables. Nests tended to be located in the upper half of the nest tree (RELHT, $\bar{x}$ = 0.62 ± 0.15) and about halfway between the main stem and the canopy edge (RELDST, $\bar{x}$ = 0.45 ± 0.23). Trees used for nesting by Scissor-tailed Flycatchers included cottonwood (*Populus deltoides*), honey mesquite (*Prosopis glandulosa*), honey locust (*Gleditsia triacanthos*), hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), osage orange (*Maclura pomifera*), pecan (*Carya illinoensis*), and oak (*Quercus* spp.).

Nest sites vs. non-nest sites.—Scissor-tailed Flycatchers chose nest trees that were taller (TREEHT, t = -4.96, $P < 0.01$) than a randomly selected group of potential nest trees (Table 4). Nest trees also had a greater density of woody stems in the >3.5-4.5, >4.5-5.5, and >5.5-6.5 m height intervals (HITSH-J, t = -3.78, -4.30, and -4.01, respectively; $P < 0.01$) compared to a random group of trees. Scissor-tailed Flycatchers also chose sites with significantly less variation in woody (WOODCOV), forb (FORBCOV), and rocky (ROCKCOV) ground cover.

The first seven components from the principal components analysis had eigenvalues greater than 1.0 and explained 78.4% of the total variance among the 21 vegetation variables. Components were interpreted as describing one or more characteristics of sites based on the relative correlations of components with original variables (Table 5). Loadings (i.e., correlations) indicated that components 1-7 generally described the following characteristics of habitat structure within the sample

area: (1) density of woody stems at intermediate height intervals and mean canopy height; (2) density of woody stems at highest height intervals; (3) amount of grass cover, amount of forb cover, amount of bare ground, density of woody stems at highest height interval, and central tree height; (4) density of woody stems at lowest height intervals and amount of woody ground cover; (5) amount of forb cover, number of trees, and distribution of trees; (6) amount of rocky ground cover; and (7) amount of bare ground.

Discriminant-function analysis incorporated components characterizing the nest tree and the area surrounding the nest tree when distinguishing between nest sites and non-nest sites (Table 6). The final model included components 2, 4, 5, and 6 that significantly discriminated between groups (Wilks' $\lambda = 0.77$; approximate $F = 9.77$, $P < 0.001$). This model correctly classified 70% of nest sites and 78% of non-nest sites, and had an overall classification accuracy of 72%. Based on the relative distributions of standardized canonical variate scores for each site (Fig. 1), nest sites tended to have taller woody vegetation, more trees surrounding the nest tree, more rocky ground cover, and less woody ground cover than did non-nest sites.

Successful vs. unsuccessful nests.—For means of variables characterizing nest concealment and isolation, there were no significant differences between successful and unsuccessful nests (Table 7). However, there was significantly less variance at successful nest sites in the distance of nests from the main stem (NESTDST; $P < 0.05$).

The principal components analysis produced nine variables with eigenvalues greater than 1.0, explaining 82.6% of the total variance among measured variables (Table 5). Loadings indicated that components 1-9 described the following

characteristics: (1) mean canopy height, density of woody stems at intermediate height intervals, and number of trees; (2) nest distance, canopy distance, density of woody stems at height intervals D and K, relative nest distance, nest height, and nest-tree height; (3) amount of grass cover, amount of forb cover, amount of leaf cover, amount of bare ground, and density of woody stems at upper height intervals; (4) density of woody stems at lowest height intervals and amount of woody ground cover; (5) relative nest height, amount of woody cover, and amount of rock cover; (6) relative nest distance and amount of forb cover; (7) number of trees, distribution of trees, and amount of wood cover; (8) amount of rock cover; (9) amount of bare ground.

Component 8 was the only composite variable entered into the discriminant-function model used to classify successful and unsuccessful nests (F-to-enter = 6.05; Wilks' $\lambda = 0.92$; approximate $F = 6.05$, $P < 0.05$). No other components met the F-to-enter criterion used to choose model variables. This model correctly classified 58% of successful and 71% of unsuccessful nests, and had an overall classification accuracy of 66%. The relative distribution of canonical variate scores showed that successful nest sites tended to have more rocky ground cover than unsuccessful nest sites (Fig. 2).

DISCUSSION

The probability of nest success on Fort Sill during this study was within the range of reported values for this species (Fitch 1950, Regosin and Pruett-Jones 1995, Nolte and Fulbright 1996). Nest loss during this study was most commonly due to predation, consistent with an earlier investigation of Scissor-tailed Flycatchers on Fort

Sill (Regosin and Pruett-Jones 1995). Because we did not observe directly any predation events during this study, we were unable to determine with certainty the type or types of predators responsible for losses in Scissor-tailed Flycatcher nests. Regosin (1994) reported observing a Cooper's Hawk (*Accipiter cooperii*) taking a single chick from a nest on Fort Sill. Other potential predators of eggs and chicks commonly observed on Fort Sill included the American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*), Great-tailed Grackle (*Q. mexicanus*), and several snake species. Mammals, such as the raccoons (*Procyon lotor*) and several species of small rodents, may also prey on nests; these were present, but rarely seen.

The primary cause of nest loss may vary among years and across this species' geographic range. Nolte and Fulbright (1996) reported that high winds and heavy rain associated with above-average rainfall were the primary causes of nest loss in southern Texas during 1992, whereas unknown causes, probably abiotic in nature, caused most losses in 1993. Climatic conditions on Fort Sill can result in significant mortality. In 1992, 25 of 35 active Scissor-tailed Flycatcher nests were lost in one severe storm (Regosin 1994). During the 1994-1996 breeding seasons, strong storms with rain and high winds moving through the study area resulted in nest loss, but these events were uncommon and highly localized (Certain pers. obs.).

Heat contributed to Scissor-tailed Flycatcher mortality on Fort Sill and may have been the proximate cause of death of eggs or chicks when nests were deserted, or when the cause was unknown. When adults were away from the nest, eggs or chicks were

several consecutive days; these temperatures are relatively common for southwestern Oklahoma in late summer.

Nest-site visitation by human observers also may influence nest success, but these effects are highly species-dependent and can vary with the type and timing of disturbance (Westmoreland and Best 1985). We rarely handled nest contents, and there was no significant difference in the mean number of days between visits between successful (3.7) and unsuccessful (3.6) nests for all years combined (t = -0.56, df = 90, P > 0.1). Also, Scissor-tailed Flycatchers are aggressive nest defenders. Adults generally stayed nearby during our visits, flew close to the nest, and often chased avian intruders away from the nest. These observations suggest that this species commonly defends the area around the nest from intrusion and from disturbance by potential predators and, thus, probably is relatively insensitive to human disturbance.

Our results support the hypothesis that Scissor-tailed Flycatchers choose nest sites that are better concealed and more isolated than are randomly selected sites. Vegetation characteristics important to nest-site selection on Fort Sill were similar to those at the Rob and Bessie Welder Wildlife Foundation Refuge in southern Texas (Nolte and Fulbright 1996). In both areas, nests tended to be placed in moderately conspicuous locations at midheight in the nest tree and halfway between the main tree stem and the canopy edge. Scissor-tailed Flycatchers at both locations chose nest trees that were taller and had more vertical cover near nest height than available trees. The reduced variation in woody and forb ground cover at nest sites, along with the tendency for these cover types to be less abundant at nest sites than at random sites (Table 4),

suggests a more homogeneous and open understory around nest trees. However, Scissor-tailed Flycatchers on Fort Sill also tended to choose nest sites that were close to other, smaller trees. Taking into account the fact that this species does not typically nest in closed forest, Scissor-tailed Flycatchers on Fort Sill appeared to choose nest sites that were intermediate along a gradient from a completely open site (with only a nest tree present) to one surrounded by closed-forest habitat. This interpretation is supported by our observation that Scissor-tailed Flycatchers most frequently nested in open forest or savanna habitats, or on the edge of more densely wooded patches.

Variables describing nest concealment and isolation were associated with nest-site selection, but were less useful at explaining variation in nest success, suggesting a need to consider alternative hypotheses. Scissor-tailed Flycatchers are aggressive nest defenders and engage in mobbing behavior towards potential predators. The quality of nest defense may better describe differences in successful and unsuccessful nests. In addition to concealment and/or isolation, Scissor-tailed Flycatchers may be selecting nest sites that allow adults to better monitor and defend nests and territories (Ricklefs 1977, Murphy 1983, Gotmark 1995, Nolte and Fulbright 1996). In this case, behavioral characteristics of individuals also play an important role in nest success. More attentive and aggressive birds would be more likely to fledge young. Nest-site selection may also be a function of access to energetic resources important to reproduction. Adult and young Scissor-tailed Flycatchers feed primarily on insects, and adults often sally from perches in or near the nest tree to capture prey (Fitch 1950, Certain pers. obs.). Nest trees surrounded by more open areas may provide a better view of and access to insect

prey than more vegetated sites.

Our results suggest that when selecting nest sites Scissor-tailed Flycatchers perceive habitat characteristics at the scale of the nest tree and at the scale of the area near the nest tree. The nest tree and nest placement within the tree appear to be chosen in part based on characteristics of concealment (greater stem density) and isolation (taller trees). Scissor-tailed Flycatchers also tended to select nest trees that were at least partially surrounded by other trees and not completely isolated in space. A further examination of habitat characteristics at progressively larger scales should better describe the configuration of woody habitats (e.g., edge vs. interior) preferred by Scissor-tailed Flycatchers and would provide a more complete picture of the cues used to choose nest sites and reduce the risk of nest predation.

ACKNOWLEDGMENTS

We thank the staff of the Natural Resources Office at the Fort Sill Military Reservation for their assistance throughout this study. We are grateful to John Ware, Bill Vieux, and David Garcia for help in the field. Financial support for this work was provided by: the U.S. Department of Defense, U.S. Army Research Office, and the Office of Naval Research (AASERT No. DAAH04-93-G-0093); the Department of Zoology, University of Oklahoma; the Oklahoma Biological Survey; and George Miksch Sutton Scholarships in Ornithology. We appreciate the comments of Mark L. Lomolino, William J. Matthews, Caryn C. Vaughn, and T. H. Lee Williams on earlier versions of this manuscript.

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FIG. 1. Frequency distribution of canonical-variate scores for Scissor-tailed Flycatcher nest sites (n = 97) and non-nest sites (n = 40). Nest sites tended to have taller woody vegetation, greater tree density, more rocky ground cover, and less woody ground cover than non-nest sites.

FIG. 2. Frequency distribution of canonical-variate scores for successful (n = 30) and unsuccessful (n = 52) Scissor-tailed Flycatcher nests. Successful nest sites tended to have greater rocky ground cover than unsuccessful nest sites.

FIG. 1.

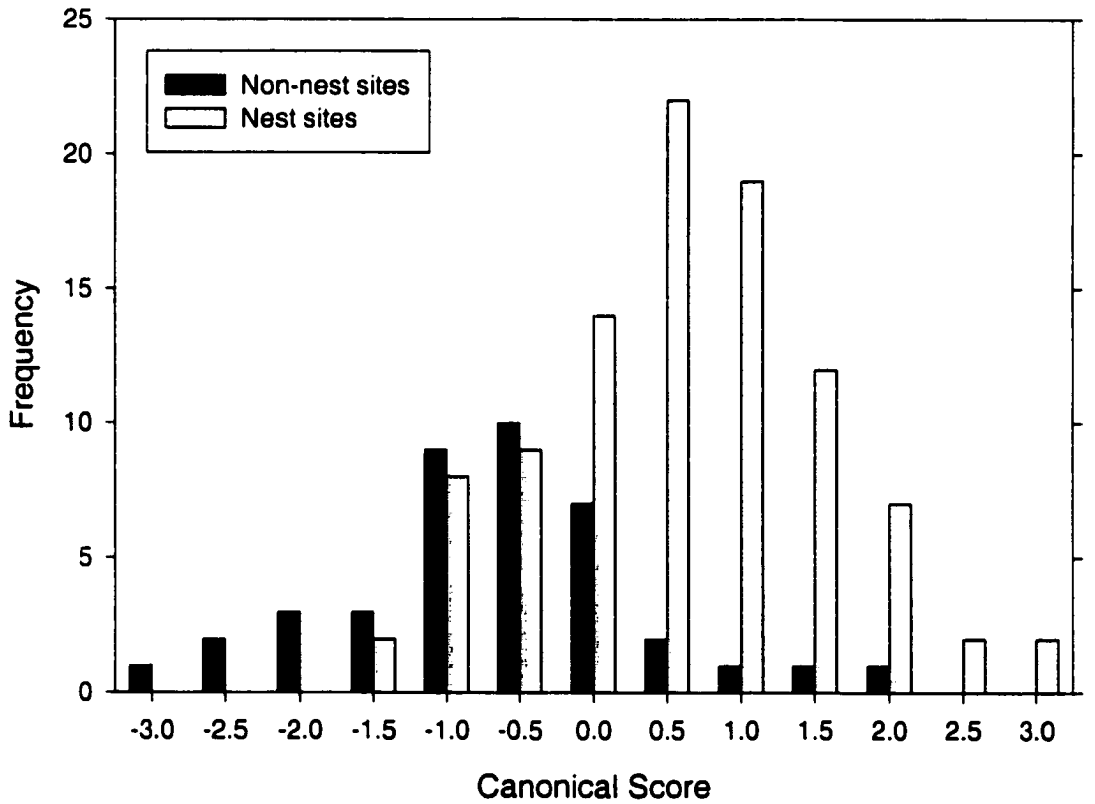
Non-nest sites
Nest sites
Frequency
25
20
15
10
5
0
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Canonical Score

FIG. 2.

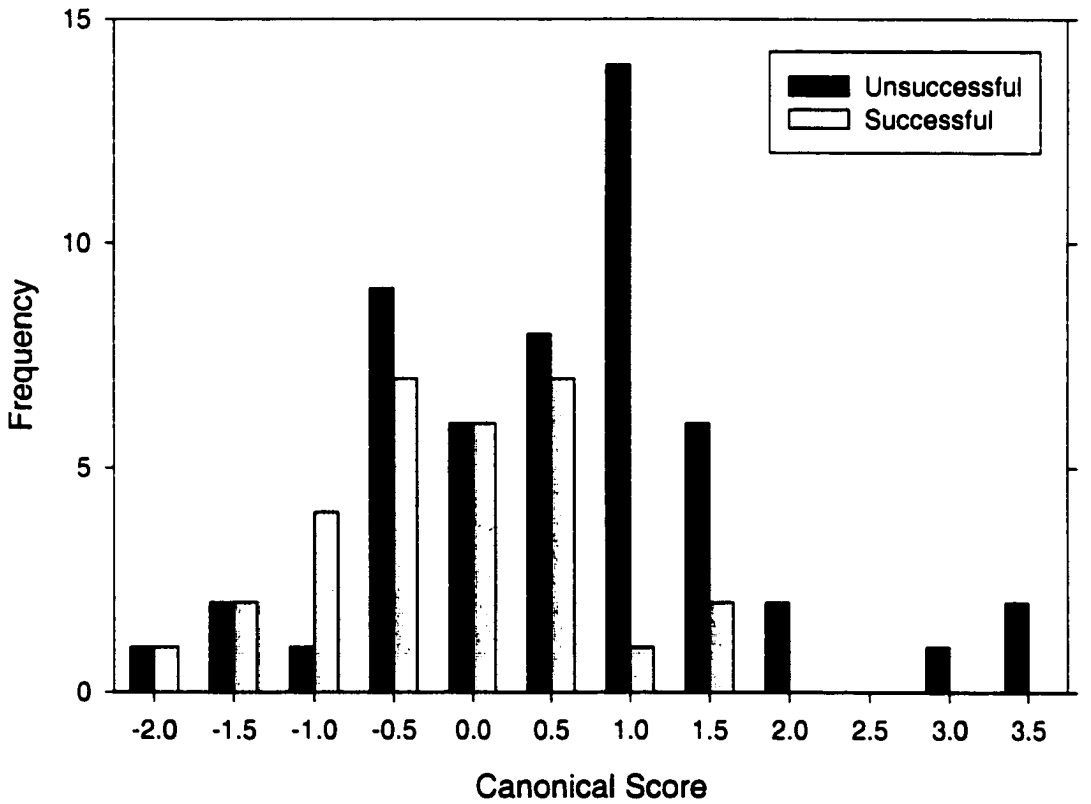
15
10
5
0
Frequency
Unsuccessful
Successful
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Canonical Score

TABLE 1. Nest placement and vegetation structure variables used to characterize degree of concealment and isolation at nest and random non-nest sites.

Variable	Description
Nest placement and cover	
NESTHT	Distance from ground to nest bottom (m)
RNESTHT	Nest height / tree height
NESTDST	Distance from main tree stem to nest edge (m)
CANDIST	Distance from main tree stem to canopy edge (m)
RNESTDST	Nest distance / canopy distance
AVGCOV	Mean concealment index
Vegetation structure	
TREEHT	Maximum nest-tree height (m)
TREETOTL	Number of trees >7.6 cm dbh
QUADCNT	Number of quadrants with trees >7.6 cm dbh
HITSA–K	Number of hits by tree stems for each height interval
CANHT	Mean canopy height for plot (m)
WOODYCOV, FORBCOV, GRASSCOV, LEAFCOV, ROCKCOV, BARECOV	Ground cover of woody plants, forbs, grass, leaf litter, rock, and bare ground (percent)

TABLE 2. Summary of reproductive data for Scissor-tailed Flycatchers on Fort Sill Military Reservation, Oklahoma, 1994-1996.

	1994	1995	1996	Total or probability
Nesting attempts monitored	31	47	52	130
Successful nests	9	16	20	45
Unsuccessful nests	22	31	32	85
Predation	15	29	25	69
Weather/starvation	3	1	1	5
Deserted	4	1	1	6
Unknown	0	0	5	5
P(nest survival during incubation) [a]	0.67	0.59	0.59	0.62
P(nest survival during nestling period) [a]	0.49	0.65	0.62	0.59
P(nest success) [a]	0.33	0.38	0.37	0.36

[a] Survival probability calculated using Mayfield method.

TABLE 3. Summary statistics of nest placement variables for Scissor-tailed Flycatcher nests on Fort Sill Military Reservation, Oklahoma, 1994-1996.

Variable	n	$\bar{x}$	SD
TREEHT (m)	93	6.91	2.04
NESTHT (m)	78	4.24	1.53
RELHT	77	0.62	0.15
CANDST (m)	82	3.56	1.64
NESTDST (m)	77	1.78	1.29
RELDST	77	0.45	0.23
AVGCOV	76	1.45	0.48

TABLE 4. Mean and standard deviation of concealment and isolation variables measured at nest and non-nest sites to test for nest-site selection.

Variable	Nest sites			Non-nest sites		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD
TREEHT[a]	98	6.86	2.00	40	5.02	1.95
TREETOT[b]	97	11.94	21.11	42	6.24	11.33
QUADCNT	97	2.10	1.54	42	1.62	1.45
HITSA[b]	98	0.44	1.13	42	0.50	2.33
HITSB[b]	98	1.36	2.47	42	1.26	2.87
HITSC[b]	98	2.38	3.85	42	1.76	2.18
HITSD[b]	98	2.87	3.59	42	1.74	2.24
HITSE[b]	98	3.00	3.89	42	2.62	3.96
HITSF[b]	98	3.28	3.87	42	2.43	4.24
HITSG[b]	98	2.88	3.02	42	2.07	3.58
HITSH[a,b]	98	5.58	5.45	42	2.74	4.62
HITSI[a,b]	98	4.71	6.20	42	1.60	3.30
HITSJ[a,b]	98	3.13	6.09	42	0.64	1.71
HITSK[b]	98	1.92	4.61	42	0.48	1.71
CANHT[a]	98	1.39	0.80	42	0.85	0.94
WOODCOV[b,c]	98	0.01	0.03	42	0.02	0.06
FORBCOV[b,c]	98	0.05	0.13	42	0.13	0.24
GRASSCOV[b]	98	0.79	0.23	42	0.69	0.27
LEAFCOV[b]	98	0.06	0.11	42	0.05	0.09
ROCKCOV[b,c]	98	0.02	0.06	42	0.06	0.14

TABLE 4. CONTINUED.

Variable	Nest sites			Non-nest sites		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD
BARECOV[b]	98	0.08	0.13	45	0.06	0.12

[a] Result of *t*-test, $P < 0.05$.

[b] Variables transformed prior to analysis (Sokal and Rohlf 1995); see Methods for details.

[c] Result of homogeneity of variance test, $P < 0.05$.

TABLE 5. Loadings, eigenvalue, and percent variance explained from principal-components analysis based on nest-placement and habitat-structure variables.[a] Results shown for variables used to test differences between nest and non-nest sites, and between successful and unsuccessful nests.

	Component								
Variable	1	2	3	4	5	6	7	8	9
				Nest vs. non-nest sites					
TREEHT	0.52	-0.38	**-0.41**	0.13	-0.05	0.06	0.15		
TREETOT	0.58	-0.27	0.36	-0.11	**0.50**	0.18	0.29		
QUADCNT	0.56	-0.22	0.30	-0.15	**0.52**	0.28	0.25		
HITSA	0.34	-0.48	-0.11	**0.66**	-0.07	0.04	0.10		
HITSB	0.50	-0.48	-0.13	**0.48**	-0.19	0.04	-0.04		
HITSC	**0.60**	-0.46	-0.05	0.14	-0.18	-0.12	-0.14		
HITSD	**0.76**	-0.26	0.21	-0.17	-0.12	-0.19	-0.10		
HITSE	**0.79**	-0.25	0.14	-0.21	-0.17	-0.16	-0.08		
HITSF	**0.73**	-0.14	0.27	-0.29	-0.21	-0.13	-0.02		
HITSG	**0.78**	0.08	0.14	-0.11	-0.05	-0.01	-0.13		
HITSH	**0.79**	0.35	0.06	0.12	-0.08	0.01	-0.03		

TABLE 5. EXTENDED.

	Component								
Variable	1	2	3	4	5	6	7	8	9
HITSI	**0.71**	**0.52**	-0.06	0.07	0.10	-0.04	0.02		
HITSJ	**0.64**	**0.57**	-0.18	0.08	-0.08	0.07	-0.01		
HITSK	0.49	**0.50**	**-0.44**	0.11	0.12	0.06	-0.20		
CANHT	**0.85**	0.18	-0.03	-0.03	0.09	0.02	0.07		
WOODCOV	0.05	-0.21	-0.16	**0.66**	0.38	-0.05	0.05		
FORBCOV	-0.12	-0.27	**-0.51**	-0.33	**0.53**	-0.24	-0.31		
GRASSCOV	-0.17	0.44	**0.75**	0.36	-0.11	-0.14	-0.08		
LEAFCOV	0.47	-0.33	-0.29	-0.18	-0.13	0.17	-0.31		
ROCKCOV	-0.05	-0.07	-0.07	-0.12	-0.29	**0.87**	-0.06		
BARECOV	0.11	-0.07	**-0.46**	-0.23	-0.32	-0.20	**0.73**		
Eigenvalue	6.77	2.52	1.96	1.70	1.35	1.14	1.02		
Variance explained (%)	32.2	12.0	9.3	8.1	6.5	5.4	4.9		
	Successful vs. unsuccessful nest sites								
TREEHT	0.51	**0.55**	-0.01	-0.15	-0.26	-0.32	-0.06	0.24	-0.20

TABLE 5. EXTENDED.

	Component								
Variable	1	2	3	4	5	6	7	8	9
NESTHT	0.54	**0.57**	-0.02	0.25	0.24	-0.31	0.12	0.24	-0.17
RELHT	0.19	0.27	0.08	**0.52**	**0.61**	-0.03	0.21	0.14	0.00
CANDST	0.24	**0.73**	-0.07	-0.32	-0.24	0.17	-0.03	-0.13	-0.17
NESTDST	0.25	**0.81**	-0.12	-0.02	0.01	0.25	0.01	-0.36	-0.15
RELDST	0.14	**0.64**	-0.13	0.15	0.17	**0.52**	0.15	-0.32	-0.04
TREETOT	**0.63**	-0.42	0.05	-0.02	-0.22	-0.16	**0.45**	-0.28	0.09
QUADCNT	0.59	-0.27	0.01	-0.06	-0.28	-0.15	**0.60**	-0.19	0.15
CANHT	**0.79**	-0.05	0.21	-0.11	-0.25	-0.05	-0.07	-0.01	0.05
HITSA	0.50	0.06	-0.22	**0.69**	-0.26	0.06	-0.04	0.04	0.13
HITSB	0.48	-0.06	-0.28	**0.63**	-0.23	0.18	0.00	0.12	0.15
HITSC	**0.73**	-0.21	-0.33	0.14	0.11	0.01	-0.05	0.22	-0.11
HITSD	**0.71**	**-0.52**	-0.08	-0.15	0.13	0.01	-0.12	0.04	-0.14
HITSE	**0.75**	-0.42	-0.18	-0.15	0.07	0.14	-0.15	-0.01	-0.17
HITSF	**0.66**	-0.39	-0.14	-0.27	0.25	0.15	-0.16	-0.04	-0.19
HITSG	**0.73**	-0.24	0.12	-0.05	0.09	0.01	-0.13	-0.09	-0.18

TABLE 5. EXTENDED.

	Component								
Variable	1	2	3	4	5	6	7	8	9
HITSH	**0.67**	-0.11	**0.46**	0.06	0.08	0.13	-0.17	0.07	0.20
HITSI	**0.68**	0.11	**0.52**	-0.06	0.17	0.00	-0.10	-0.12	0.18
HITSJ	0.53	0.32	**0.57**	-0.18	0.13	0.01	0.01	-0.06	0.17
HITSK	0.41	**0.60**	**0.41**	-0.06	0.05	-0.22	0.03	0.09	0.05
WOODCOV	0.16	0.10	0.03	**0.41**	**-0.40**	-0.27	**-0.53**	-0.33	-0.09
FORBCOV	0.09	0.23	**-0.53**	-0.11	0.16	**-0.50**	0.14	-0.11	-0.24
GRASSCOV	-0.38	-0.36	**0.66**	0.30	0.10	0.04	0.07	-0.12	-0.27
ROCKCOV	0.04	0.25	0.24	-0.18	**-0.42**	0.34	0.15	**0.58**	-0.10
LEAFCOV	0.47	-0.06	**-0.52**	-0.11	0.05	0.30	0.11	0.06	0.01
BARECOV	0.14	0.27	**-0.44**	-0.29	0.18	-0.13	-0.22	0.02	**0.65**
Eigenvalue	6.90	4.06	2.60	1.94	1.46	1.30	1.16	1.07	1.00
Variance explained (%)	26.5	15.6	10.0	7.5	5.6	5.0	4.5	4.1	3.9

*Relatively high absolute loadings (component 1, > |0.6|; 2, > |0.5|; 3-9, > |0.4|) in bold.

TABLE 6. Statistics for stepwise discriminant analysis of nest sites and non-nest sites. Results are for analysis using principal components. Variables listed in order entered into model.

Variable	*F*-to-enter value	Standardized canonical-discriminant function	Classification function[a]	
			Nest sites	Non-nest sites
Component 4	14.61	0.63	-0.23	0.56
Component 5	8.80	0.41	-0.12	0.37
Component 2	8.46	0.52	-0.18	0.47
Component 6	4.18	0.38	-0.14	0.32
Constant			-0.75	-1.06

[a] Tabulated values used with original values for variables. Products of corresponding measurements and function values summed and then added to constant. Site classified into particular group based on which classification function produces highest value.

TABLE 7. Mean and standard deviation of variables used to test differences between successful and unsuccessful nests, 1994-1996.

Variable	Successful nests			Unsuccessful nests		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD
TREEHT	32	6.74	1.92	61	7.00	2.11
NESTHT	30	4.29	1.51	48	4.21	1.56
RELHT*	30	0.65	0.15	47	0.61	0.14
CANDST	30	2.87	1.21	52	3.96	1.73
NESTDST*	30	1.39	0.94	47	2.02	1.43
RELDST*	30	0.44	0.23	47	0.46	0.24
AVGCOV	30	1.38	0.42	46	1.50	0.51
TREETOTL*	30	12.50	21.74	60	13.15	23.39
QUADCNT	30	1.97	1.63	61	2.15	1.53
CANHT	28	1.32	0.84	60	1.44	0.82
HITSA*	28	0.46	1.20	60	0.43	1.10
HITSB*	28	1.82	3.16	60	1.07	1.97
HITSC*	28	2.04	3.78	60	2.37	3.50
HITSD*	28	2.96	3.56	60	2.88	3.81
HITSE*	28	2.82	2.74	60	3.27	4.54
HITSF*	28	2.89	2.63	60	3.43	4.45
HITSG*	28	2.64	3.06	60	3.12	3.07
HITSH*	28	5.75	5.20	60	5.78	5.79
HITSI*	28	4.14	5.51	60	5.27	6.81
HITSJ*	28	2.46	2.98	60	3.68	7.43
HITSK*	28	1.50	3.38	60	2.30	5.34

TABLE 7. CONTINUED.

Variable	Successful nests			Unsuccessful nests		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD
WOODCOV[a]	29	0.01	0.06	60	0.01	0.04
FORBCOV[a]	29	0.02	0.04	60	0.04	0.08
GRASSCOV[a]	29	0.76	0.24	60	0.80	0.20
ROCKCOV[a]	29	0.03	0.08	60	0.01	0.05
LEAFCOV[a]	29	0.08	0.14	60	0.05	0.10
BARECOV[a]	29	0.10	0.17	60	0.08	0.12

[a] Variables transformed prior to analysis (Sokal and Rohlf 1995); see Methods for details.

[b] Result of homogeneity of variance test, $P < 0.05$.

David L. Certain • Gary D. Schnell

Nest-site selection and nest predation in a prairie landscape mosaic

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Abstract Nest predation is a major cause of mortality in birds, and habitat fragmentation has been shown to be associated with higher rates of nest predation in forested habitats. We investigated the relative importance of landscape characteristics, including fragmentation, in nest-site selection by and nest predation on a prairie species, the scissor-tailed flycatcher (Tyrannus forficatus). Percent open country, area of open country, area of closed forest, area of savanna, and length of woody edge were measured for three nested, circular sample units (100-m, 250-m, and 500-m radius) centered on trees at nest sites and at random sites. We also measured distance from each nest and random site to the nearest woody edge to investigate the effect of edge proximity. Scissor-tailed flycatchers chose nest sites that were less fragmented, had less closed forest and savanna habitat, and had shorter total woody edge than expected by chance. Patterns in landscape measures across scales indicated that scissor-tailed flycatchers tended to avoid open areas adjacent to or imbedded within relatively large woody patches. They chose nest sites further from the nearest woody edge than expected by chance. Successful nest sites had less woody edge than depredated nests. These results show that structural characteristics of the landscape surrounding nest sites can have a significant influence on habitat choice and fitness in birds. Our data also support previous findings that edge habitats have negative effects on reproductive success of breeding birds and indicate that birds nesting in prairie habitats face some of the same selective pressures as those nesting in fragmented forest landscapes.

Key words Nest predation • Prairie fragmentation • Scissor-tailed flycatcher • Scale effects • Oklahoma

Introduction

Nest predation is a major cause of mortality in breeding birds (Ricklefs 1969) and has received considerable attention as a possible contributing factor to the decline of migratory songbirds in North America (e.g., Wilcove 1985; Donovan et al. 1995; Robinson et al. 1995; Morse and Robinson 1999) . Historical and contemporary modifications of natural landscapes, primarily through forest fragmentation, have led to an increase in the patchiness of woody habitats and the amount of woody edge. Most studies of nest predation and the effects of modified landscapes on reproductive success have focused on species in forested landscapes (e.g., Andren 1992; Robinson et al. 1995; Tewksbury 1998; Morse and Robinson 1999). Much of the North American prairie ecosystem also has undergone a transformation through land conversion for agriculture and fire suppression, resulting in a more highly fragmented system than originally existed (Robertson et al. 1997). In some prairie landscapes, man-made woody habitats (e.g., windbreaks and fencerows) have increased fragmentation. However, we still know little about the effects of these habitat modifications and the role of nest predation in the productivity of prairie species. Studies of landscape effects on predation of prairie birds are uncommon and, generally, have been limited to the effects of the size of the habitat patch within which nests are located and the influences of the proximity of nests to an edge (Johnson and Temple 1986; Møller 1989; Vickery et al. 1992; Burger et al. 1994).

Newly created edge environments in forested landscapes may act as "ecological traps" (Gates and Gysel 1978), attracting nesting birds that may not have appropriate nest-defense strategies for areas with a high diversity and abundance of potential nest predators. However, a significant debate continues as to the influence of landscape composition (e.g., mostly forested v. highly fragmented) on biotic edge effects (e.g., Andren 1992; Hartley and Hunter 1998). Edge effects on species nesting in open habitats outside of woody patches are even less well understood.

The density and diversity of many nest predators (e.g., snakes, mammals, birds) is thought to be greatest along the edge compared to the interior of woody patches (Robbins 1980; Whitcomb 1981; Wilcove 1985; Andren 1992; Marini et al. 1995). However, since nest predators also exist in the interior of woody patches, both edge and interior are sources of predators for the surrounding habitat. This suggests that the total area of woody habitat, as well as the proximity or amount of edge habitat, near a nest site may influence the probability of nest success.

Under conditions of high nest-predation rates, natural selection should be strong for traits that reduce the susceptibility of eggs and nestlings to predation. One way for birds to reduce nest predation is through nest-site choice. Typically, investigations of nest-site selection and nest predation have focused on characteristics of habitat structure at scales no larger than a single territory or a nest patch. However, several studies have demonstrated the hierarchical nature of nest-site selection in birds (e.g., Martin and Roper 1988; Bergin 1992) and the influence of landscape characteristics on nest success (e.g., Wilcove 1985; Small and Hunter 1988; Andren 1992; Breininger et al. 1995;

Robinson et al. 1995; Tewksbury et al. 1998).

We investigated the importance of prairie-landscape characteristics to nest-site selection and the probability of predation for nests of the scissor-tailed flycatcher (Tyrannus forficatus). This Neotropical migrant breeds in open habitats in Texas, Oklahoma, and Kansas, as well as parts of New Mexico, Colorado, Nebraska, Missouri, Arkansas, and Louisiana (Fitch 1950, AOU 1998, Regosin 1998). In a previous study of the scissor-tailed flycatcher in southwestern Oklahoma (Certain and Schnell 2000), nest predation was indicated in 81% of all nest losses and was the primary cause of nest loss in each of three years. For the current analysis, we predicted that nest sites would be located in landscapes with more open habitat, and less woody vegetation and edge habitat than a random selection of potential nest sites. We also hypothesized that nests would be further away from the nearest woody edge than expected by chance. We predicted that, on average, these same characteristics would be shared by successful nest sites when compared to depredated nest sites.

Materials and methods

Study area

This study was conducted on the Fort Sill Military Reservation, Comanche County, in southwestern Oklahoma. The landscape was a complex mosaic of a mixed- and short-grass prairie with numerous small woody patches and some more extensive woodlands, particularly adjacent to water courses. Woody patches were both natural and man-made; they included mesquite and oak savanna, fencerows, riparian woodland, crosstimbers forest, and bottomland forest (Pogue 1998). The land adjacent to, but outside the Fort Sill boundary, was a more homogeneous mix of primarily cropland and rangeland (for more information, see Pogue 1998).

Many of the potential predators on eggs or chicks in scissor-tailed flycatcher nests found on Fort Sill were associated with woody habitats. These included several species of birds (e.g., Cooper's hawk [Accipiter cooperii], American crow [Corvus brachyrynchos], blue jay [Cyanocitta cristata]), mammals (e.g., raccoon [Procyon lotor]) and snakes (e.g., black rat snake [Elaphe obsoleta], coachwhip [Masticophis flagellum]).

Nest sampling

We monitored nesting attempts by scissor-tailed flycatchers between early May and late July of 1994-1996. The sampling area was searched both by driving roads and walking through roadless areas. Nests were located by searching trees and shrubs, and by following adults until they returned to a nest site. Areas that were off-limits on the military reservation (e.g., live-fire zones) or that could not be accessed on a regular basis were excluded from the sampling region. Some land-cover types were not extensively sampled because they represented habitat types not typically exploited by scissor-tailed flycatchers (e.g., cross-timbers, bottomland). However, we did search for nests along the edges of these land-cover types. We also excluded from analyses nest sites found in the area of the reservation where developed and landscaped areas were the dominant land-cover type. While scissor-tailed flycatchers sometimes exploit man-made platforms (e.g., telephone poles, wind socks) for nesting, we chose not to incorporate nests built on artificial structures in our study. As a result of exclusions, the actual sampling area included about one-third (ca. 12,600 ha) of the total area of Fort Sill. All of the most extensive land-cover types found on the reservation were represented in our sampling area.

At the time each nest was found, the number of eggs or nestlings was recorded, and nests were revisited every 2-8 days ($\bar{x} = 3.6$) until the outcome of the nesting attempt was determined. Nests were considered to be successful if at least one chick fledged.

Landscape sampling

We used a 10-m-resolution, reclassified land-cover map of Fort Sill and an 8-km-wide zone surrounding Fort Sill to evaluate landscape structure around nest sites and around 500 random sites chosen from within the nest-sampling area. Most landscape studies of nest predation have evaluated landscape patterns around habitat patches (that may contain a number of nests), with patches defined as areas of relatively homogeneous vegetation type surrounded on all sides by unlike vegetation or land-cover types. However, grasslands on Fort Sill typically are not isolated patches, but exist as relatively large, contiguous tracts. We measured landscape structure within circular sampling areas centered on individual nest trees and on trees at random sites.

Landscape measures were calculated using the Geographic Resources Analysis Support System (GRASS ver. 4.1; CERL 1989) software and the r.le sub-program (Baker and Cai 1992) on a raster-based digital map created by digitizing black-and-white aerial photography (Pogue 1998). The original land-cover map was reclassified into five general land-cover types (open country, savanna, closed forest, water, urban/developed) from an original classification of 15 to increase interpretibility and to reflect similarity of woody land-cover types as potential sources of nest predators (Table 1 equates original land-cover categories with reclassified categories).

Landscape variables measured at each site included: (1) percent open country; (2) area open country; (3) area closed forest; (4) area savanna; (5) area closed forest + savanna; and (6) total length of edge where open country and woody land-cover types

adjoined. Percent open country was used as a general measure of landscape fragmentation, consistent with the use of percent forest cover used in studies of forest fragmentation and avian productivity (e.g., Andren 1992; Donovan et al. 1995; Robinson et al. 1995; Tewksbury et al. 1995). We tested for the individual effect of closed forest area and the combined effects of the area of closed forest plus savanna habitats, since observations suggested that predators used both of these habitats.

Our measure of the total length of edge between woody (i.e., closed forest and savanna) and open habitats was used to estimate physical characteristics of edges in the landscape. This is in contrast to the measure of nest distance from an edge, which provides little information about edge structure. We chose to measure only the "hard edge" between closed forest or savanna and open country because this is where predators were likely to be most abundant (e.g., Wilcove 1985; Andren 1992).

Variables were evaluated within each of three progressively larger circular sample units, each centered on a nest tree or the tree nearest to a randomly selected point. The sample units had radii of 100 m (2.93 ha), 250 m (18.85 ha), and 500 m (77.05 ha). The progressively larger sample units were used to investigate the relative importance of landscape variables with increasing sample area. Percent open country was the ratio of open-country pixels (1 pixel = 0.01 ha) within each sample unit to the total number of pixels. Values for the area of open country, closed forest, and savanna were each calculated based on the total number of pixels classified in each respective land-cover type. Total edge length was calculated by counting the number of times open-country and closed forest or savanna pixels shared a common pixel edge and

multiplying that value by the length of a pixel edge (10 m). The shared corner of two pixels (diagonal adjacency) was not counted as an edge.

We used the entire land-cover map of Fort Sill and the surrounding landscape as a single sample unit to measure the distance from each nest tree to the edge of the nearest forest or savanna patch. In this way, we did not restrict nearest-neighbor analysis to only those pixels within a circular sample unit.

Statistical analysis

We employed a resampling procedure (Simon 1997) using Resampling Stats (Resampling Stats, Inc. 1997) to examine differences in means of variables between nest and random sites, and between successful and depredated nests. Resampling does not require *a priori* assumptions about how data are distributed. To test for differences in means between nest (n = 92) and random (n = 500) sites, we first combined the sample records for the two groups in a random order, and then partitioned all of the records from the combined dataset into two new samples equal in size to the original groups. We then calculated the difference in means between the two new samples and compared that difference to the difference in means of the original samples. We repeated this process 1000 times for each variable and at each scale. Tests of means for successful and depredated nests followed a similar procedure, but we resampled from a dataset produced by combining the two original samples for successful (n = 32) and depredated (n = 52) nests. P-values

produced by this technique are exact and are based on the number of times that the difference between the two new samples exceeds the difference between the means of the two original samples. Because we were only interested in statistical deviations in one direction for each variable, as described in our predictions, all tests were one-tailed (Sokal and Rohlf 1995).

Scissor-tailed flycatchers may renest within the same territory both within and between years (Regosin and Pruett-Jones 1995). If all nests found were incorporated into our samples, this behavior could result in a reduction of the independence of the overall sample, since we were unable to recognize individuals and track renesting attempts. We addressed this potential statistical dependence within our dataset by including only the first nest found in any individual nest tree, with second nests being eliminated (whether from the same year or a subsequent year). We also randomly removed all but one nest site from each group of nests that were located within 100 m of each other, both within and among years.

Results

Nest sites (n = 92) had a greater percentage and larger area of open country, less area of closed forest, less area of closed forest + savanna cover, and shorter total woody-edge length than random sites (n = 500) at all three sample scales ($P < 0.05$; Table 2). The

area of savanna habitat was significantly different between nest and random sites at the 500-m scale. Nest sites also were located further from the nearest woody patch ($\bar{x}$ = 368.11, SD = 482.21) than were random sites ($\bar{x}$ = 248.89, SD = 261.54; $P < 0.01$).

Total edge length was significantly shorter ($P < 0.05$) near successful nests (n = 32) than depredated nests (n = 52) at the 100-m scale, but not at the 250-m and 500-m scales (Table 3). Successful nests tended to be further away from the nearest woody patch ($\bar{x}$ = 417.27, SD = 522.01) than did depredated nests ($\bar{x}$ = 294.72, SD = 358.50), but not significantly so ($P = 0.09$).

The difference between nest and random sites in means of most landscape variables diverged with increasing scale (Fig. 1). The exception to the pattern of diverging means was for percent open country (Fig. 1A). The percent of open-country habitat slightly decreased with sample area at both nest and random sites. Differences in area of open country, closed forest, savanna, closed forest + savanna, and length of woody edge all increased as the scale of measure increased (Fig. 1B-F).

Relative changes in values of landscape measures between successful and depredated nest sites (Fig. 2) show few consistent patterns across scales. The lack of any statistically significant differences between groups (except for length of woody edge at 100-m radius scale) suggests that resultant patterns seen in Fig. 2 are due to random processes.

Discussion

Nest-site selection

Scissor-tailed flycatchers generally are described as open-country nesters (Fitch 1950; Regosin 1998), which is supported by our results. They appeared to choose open nest sites that were isolated from the nearest woody edge, had little closed forest or savanna vegetation, and had little woody edge. Our findings also support those of previous studies demonstrating that habitat characteristics of the landscape are important to nest-site selection in birds (e.g., Storch 1991; Hunter et al. 1995).

Other factors, not necessarily exclusive of predation risk, may influence nest-site selection and, ultimately, nest success. These include access to resources and the ability to view the surrounding environment. Adult and young scissor-tailed flycatchers feed primarily on insects, and adults often sally from perches in or near the nest tree to capture prey (Fitch 1950; Certain pers. obs.). Nest trees surrounded by open, grassy areas, as most of our nest sites were, allow for a better view of and easier access to insect prey than would more vegetated sites. The open sites scissor-tailed flycatchers prefer allow them readily to observe potential predators near the nest (Götmark et al. 1995). They choose nest sites with characteristics of the landscape affecting both predator avoidance and resource availability.

Nest predation

Results of studies in fragmented forests generally have shown that rates of nest predation on forest birds increase with decreasing forest cover (Andren 1992; Donovan et al. 1995; Robinson et al. 1995). Nest predation on scissor-tailed flycatchers, a prairie bird, also was associated with habitat fragmentation that, in part, was the result of encroaching woodland and woody edges. The significant effect of edge length on nest predation, in our study, adds support to the supposition that habitat edges can have a negative impact on avian productivity. If nest predators are attracted to edge environments (because of foraging, nesting, and/or roosting), landscapes with a greater total edge length will tend to have a higher abundance of nest predators.

Scissor-tailed flycatchers selected nest sites isolated by distance from the nearest woody edge, and nests closer to edges tended to have higher nest predation (albeit the difference was not quite significant statistically). The type of nest predator may influence the importance of nest proximity. Highly mobile predators, such as birds, would be expected easily to move relatively long distances between nest sites and woody patches. Burger et al. (1994) reported higher predation rates for artificial nests in prairie fragments <60 m from woody cover. Johnson and Temple (1986) also showed reduced productivity for artificial nests <45 m from a forest edge. Scissor-tailed flycatcher nests that we found on Fort Sill were most often located at even greater distances than these from the nearest woody edge ($\bar{x}$ = 356 m).

Scale effects

Our results showed a pattern of diverging means of landscape variables between nest sites and random sites as sample-unit area increased (Table 2, Fig. 1). Scissor-tailed flycatchers tended to avoid open areas that were adjacent to or imbedded in relatively large tracts of woody habitat (the presence of such large tracts would be reflected mainly when habitat measures are taken at larger scales), preferring open areas that extend considerably beyond the immediate nest site.

The finding of greater differences in landscape characteristics between nest and random sites with increased scale contrasts with the finding of Hunter et al. (1995), who calculated landscape metrics around northern spotted owl (Strix occidentalis caurina) nest sites and around random sites. Their results showed most measures of landscape structure to be convergent as sample area increased. One difference between these two studies is that our largest sample area (77.05 ha) was much smaller than their smallest (200 ha). Significant differences in vegetation composition and fragmentation between nest and random sites for northern spotted owls existed for multiple sample unit areas, up to 803 ha (Hunter et al. 1995). For scissor-tailed flycatchers, significant differences in landscape measures between nest and random sites existed at all sample unit sizes (Table 2).

In our tests of successful and depredated nest sites, edge length, the one statistically significant variable, differed at the smallest sample-unit area (Table 3). Only woody edges closest to nests had a significant association with nest success. One

possible interpretation is that this is due to foraging patterns of nest predators, such that they have the greatest affect on nest success within a limited area around their own nesting or roosting site.

Previously, Certain and Schnell (2000) demonstrated the effect of local-scale habitat characteristics (e.g. nest tree height, density of woody vegetation surrounding nest cup, presence of trees near nest) on nest-site selection and nest success of scissor-tailed flycatchers. Results of the current investigation indicate that scissor-tailed flycatchers on Fort Sill also use characteristics of the landscape to choose nest sites, and that one of these characteristics (edge length) was associated with a risk of predation and reproductive success. Our results also support the idea that habitat edges, especially "hard edges" between open and woody habitats, can negatively influence birds nesting in nonforest or open habitats. These findings suggest that landscape-scale habitat structure can be important to nest-site selection, to nest success, and potentially to long-term population success. Increases in the amount of edge in a prairie landscape may lead to increased predation pressure and reduced productivity for breeding birds.

Acknowledgements We thank the staff of the Natural Resources Office at the Fort Sill Military Reservation for their assistance throughout this study. We are grateful to John Ware, Bill Vieux, and David Garcia for help with field work. Financial support for this work was provided by: U.S. Department of Defense, U.S. Army Research Office, and Office of Naval Research (AASERT No. DAAH04-93-G-0093); Department of Zoology, University of Oklahoma; Oklahoma Biological Survey; and George Miksch

Sutton Scholarships in Ornithology. We also appreciate the comments of Mark V. Lomolino, William J. Matthews, Caryn C. Vaughn, and T. H. Lee Williams on earlier versions of this manuscript.

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Fig. 1 Plots of landscape variable means (± SE) for nest sites (n = 92) and random sites (n = 500) versus sample-unit area

Fig. 2 Plots of landscape variable means (± SE) for successful (n = 32) and depredated (n = 52) nest sites versus sample-unit area

FIG. 1

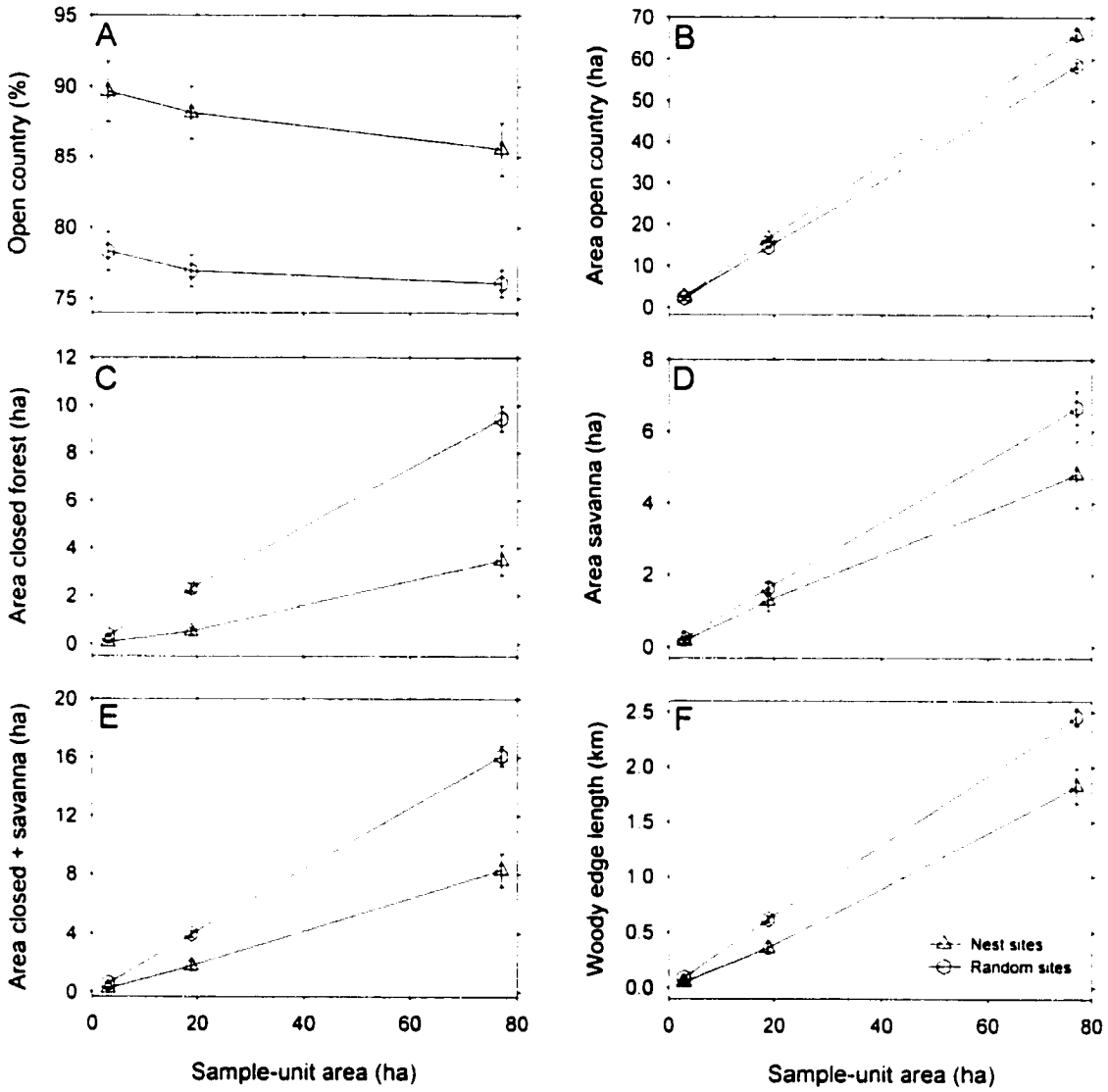
A
B
C
D
E
F
Open country (%)
Area open country (ha)
Area closed forest (ha)
Area savanna (ha)
Area closed + savanna (ha)
Woody edge length (km)
Nest sites
Random sites
Sample-unit area (ha)
Sample-unit area (ha)

FIG. 2

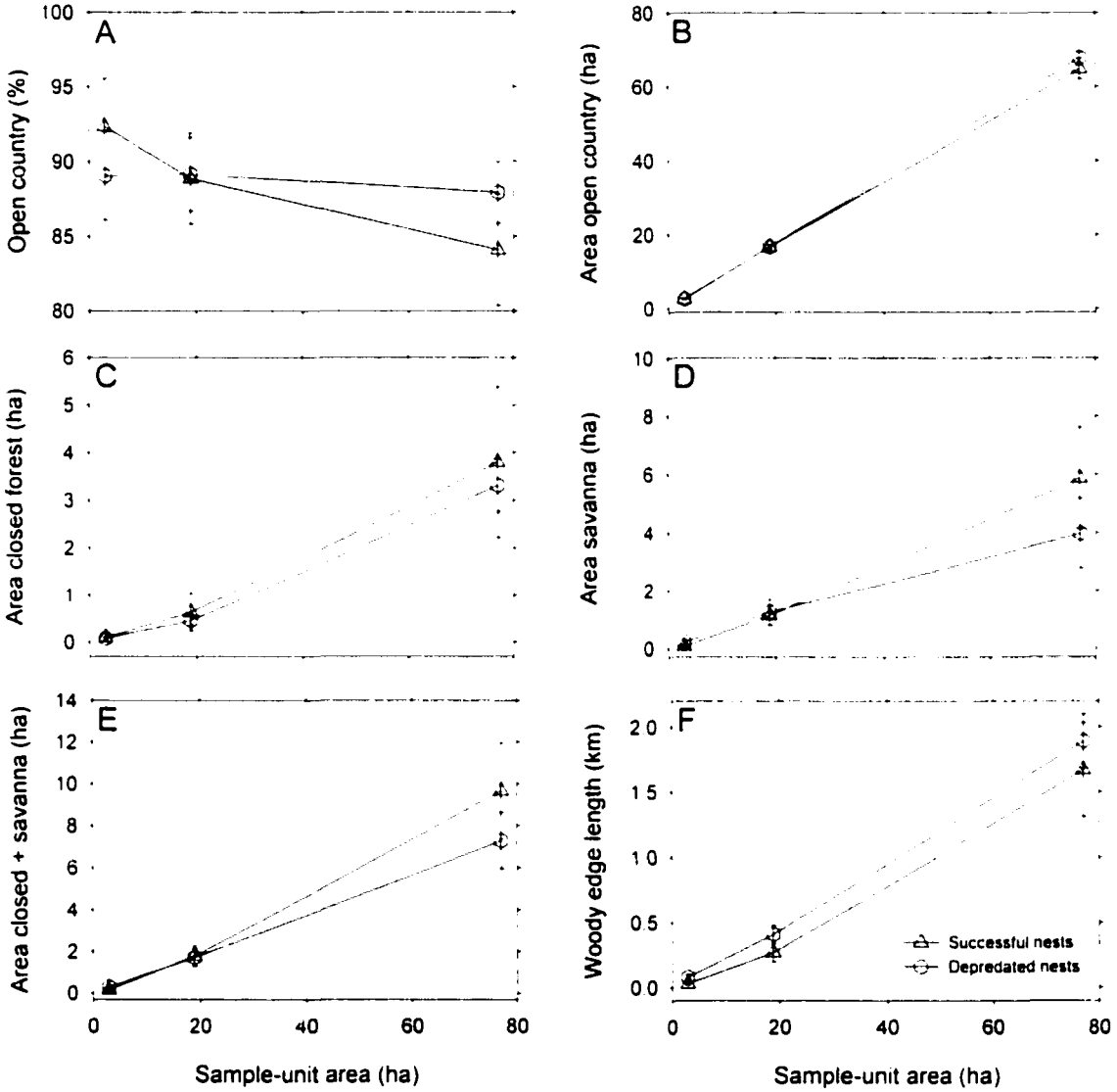
A
B
C
D
E
F
Open country (%)
Area open country (ha)
Area closed forest (ha)
Area savanna (ha)
Area closed + savanna (ha)
Woody edge length (km)
Sample-unit area (ha)
Sample-unit area (ha)
Successful nests
Depredated nests

Table 1 Land cover categories for original Fort Sill classification (Pogue 1998) and reclassified map

Original category	Reclassified category
Short grass	Open country
Mixed grass	Open country
Tall grass	Open country
Rangeland	Open country
Agriculture	Open country
Mesquite savanna	Savanna
Oak savanna	Savanna
Cross timbers	Closed forest
Bottomland forest	Closed forest
Riparian	Closed forest
Tree plot	Closed forest
Osage orange/locust/elm	Closed forest
Water	Water
Cantonment [a]	Urban/developed
Disturbed area	Open country

[a] Residential and built-up area of Fort Sill where developed and landscaped areas were dominant

Table 2 Mean (SD) of variables measured at three scales to test for nest-site selection. Sample units were centered on trees at nest sites (n = 92) and at random points (n = 500) within overall sampling area. Significantly different ($P < 0.05$) means in *bold type*

	Scale*					
	100 m		250 m		500 m	
Variable	Nest	Random	Nest	Random	Nest	Random
Percent open country	**89.63**	**78.32**	**88.13**	**76.95**	**85.57**	**76.09**
	(20.70)	(30.60)	(18.06)	(25.31)	(17.89)	(21.53)
Area open country (ha)	**2.63**	**2.30**	**16.58**	**14.51**	**65.93**	**58.63**
	(0.06)	(0.04)	(0.35)	(0.21)	(1.44)	(0.74)
Area closed forest (ha)	**0.08**	**0.35**	**0.53**	**2.32**	**3.50**	**9.46**
	(0.28)	(0.72)	(1.41)	(3.68)	(6.10)	(12.11)
Area savanna (ha)	0.17	0.24	1.28	1.63	**4.81**	**6.67**
	(0.51)	(0.61)	(2.78)	(3.16)	(8.97)	(10.54)
Area closed forest +	**0.25**	**0.60**	**1.80**	**3.95**	**8.31**	**16.13**
savanna (ha)	(0.56)	(0.89)	(2.93)	(4.65)	(10.75)	(15.55)
Edge length (km)	**0.054**	**0.092**	**0.356**	**0.620**	**1.832**	**2.457**
	(0.012)	(0.016)	(0.434)	(0.688)	(1.511)	(1.836)

* Radius of circular sample unit

Table 3 Mean (SD) of variables measured at multiple scales to test for influence on nest success. Sample units were centered on successful (n = 32) or on depredated (n = 52) nests. Significantly different ($P < 0.05$) means in *bold type*

	Scale*					
	100 m		250 m		500 m	
Variable	Successful	Depredated	Successful	Depredated	Successful	Depredated
Percent open country	92.36	89.06	88.88	89.17	84.10	87.95
	(18.16)	(21.37)	(17.15)	(17.71)	(21.16)	(14.84)
Area open country (ha)	2.71	2.61	16.75	16.81	64.80	67.77
	(0.09)	(0.09)	(0.57)	(0.46)	(2.88)	(1.59)
Area closed forest (ha)	0.10	0.08	0.63	0.46	3.80	3.31
	(0.44)	(0.15)	(2.27)	(0.59)	(8.97)	(3.99)
Area savanna (ha)	0.08	0.22	1.15	1.26	5.87	3.98
	(0.20)	(0.63)	(1.98)	(3.19)	(9.89)	(8.64)
Area closed forest + savanna (ha)	0.17	0.30	1.79	1.72	9.67	7.29
	(0.47)	(0.62)	(2.80)	(3.08)	(13.01)	(9.67)
Edge length (km)	**0.028**	**0.078**	0.274	0.405	1.674	1.890
	(0.072)	(0.138)	(0.380)	(0.471)	(1.470)	(1.527)

* Radius of circular sample unit

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Range-wide spatial patterns in landscape structure and population abundance of the scissor-tailed flycatcher

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Abstract Geographic-scale avian abundance patterns have been hypothesized to be the result of the degree to which local habitats meet species niche requirements. Characteristics of landscape structure (e.g. fragmentation) may influence local abundance through associated changes in rates of nest predation and nest parasitism. Measures of landscape structure have been shown to be associated with the relative abundance of breeding birds over large geographic areas. Previous investigations into the relationships between landscape structure and avian abundance have not explicitly tested for associations over the geographic range of a species. In addition, these studies have focused almost exclusively on forest-dwelling species of eastern deciduous forests. We used Breeding Bird Survey (BBS) data and digital habitat maps to examine associations of measures of landscape structure and composition with the relative mean abundance of the scissor-tailed flycatcher, an open-country nester. The 200 BBS routes used in the analysis were scattered over most of the scissor-tailed flycatcher's primary breeding range, which includes parts of Arkansas, Kansas, Louisiana, Missouri, Oklahoma, and Texas. Composite variables from principal components analysis of the original data were significantly associated with abundance. Spatial structure in ecological data, in the form of autocorrelation, can result in significant associations between variables. Relative abundance and component scores exhibited significant spatial autocorrelation. However, differences in component scores remained significantly associated with differences in abundance after allowing for spatial structure. These results suggest that landscape structure influences local avian abundance and range-wide abundance patterns, most likely via influence on local

reproductive success.

Key words Landscape structure • Avian abundance • Scissor-tailed flycatcher • Autocorrelation

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Introduction

Characteristics of landscape-level habitat structure, especially the degree of habitat fragmentation, have been linked to the reproductive success of migratory birds in forested landscapes (Robinson et al. 1995). Several measures of landscape structure, including fragmentation, also have been shown to be associated with the abundance and population change of Neotropical migrants over a large geographic area (Flather and Sauer 1996). These associations suggest the importance of local ecological processes in determining geographic abundance patterns (Brown 1984, Brown et al. 1995). However, previous landscape-level studies have not explicitly modeled associations of landscape structure and population parameters across a species' geographic range. In addition, most investigations into the influence of landscape structure on breeding birds, especially Neotropical migrants, have focused on forest-dwelling species in eastern deciduous forests of the United States. Few data exist for landscape characteristics and the associations of those characteristics with breeding bird abundance in prairie or more naturally fragmented habitats, like those found throughout much of the south-central

U. S.

Spatial structure is a common and often important characteristic of ecological datasets. Examinations of the spatial structure of populations on a regional scale have become more common with the increased availability of datasets like the North American Breeding Bird Survey (BBS) and the increased use of spatial statistics in ecological studies. Large-scale data on habitats and vegetation structure have also increased in availability and use due to reduced cost of remotely-sensed data (e.g. satelite imagery, aerial photography), to improvements in computer processing power, and to increased training of ecologists in the use of appropriate tools and data sources.

In this study, we described elements of landscape structure at BBS routes throughout much of the range of the scissor-tailed flycatcher (Tyrannus forficatus). We also investigated landscape-level habitat correlates of scissor-tailed flycatcher abundance by examining omnidirectional and directional patterns of composite measures of landscape structure. Local environmental conditions, as described by the structure and composition of general vegetation types surrounding BBS routes, should exhibit similar patterns of spatial structure (e.g. autocorrelation) if measured parameters are important in determining local abundance.

Materials and methods

The scissor-tailed flycatcher is a Neotropical migrant that breeds primarily in open habitats throughout Texas, Oklahoma, and Kansas and parts of New Mexico, Colorado, Nebraska, Missouri, Arkansas, and Louisiana (Fitch 1950, AOU 1998, Regosin 1998). Previous studies of this species in Oklahoma and Texas demonstrated the importance of nest predation as a cause of mortality among young (Regosin and Pruitt-Jones 1995, Nolte and Fulbright 1996, Certain 2000). Certain (2000) also showed that several measures of landscape structure were important to nest-site selection (percent open-country habitat, area of open-country and woody habitats, total length of woody-edge habitat) and that the landscape surrounding nests lost to predators had significantly more woody edge than did landscapes surrounding successful nests. These findings suggested that differences in landscape structure may be important to the relative local abundance of scissor-tailed flycatchers, and may help explain its' geographic patterns of abundance.

Abundance Data

We used BBS data to estimate the relative mean abundance of scissor-tailed flycatchers across their breeding range in the United States from 1985 to 1994. The BBS program is coordinated through the U. S. Geological Survey and the Patuxent

Wildlife Research Center and consists of approximately 3,500 roadside surveys established in the U. S., Canada, and Mexico. Each BBS route is 39.4 km long and generally follows secondary roads. In June of each year, observers drive designated routes, stopping every approximately 0.8 kilometers to record all birds seen or heard (for more information on BBS methods see Sauer et al. 1999). Approximately 226 BBS routes have been established and surveyed at least once within the breeding range of the scissor-tailed flycatcher. We excluded from analyses routes surveyed fewer than five times during the 10-yr study period. Other routes were excluded because aerial photographs, used to measure landscape structure (see next subsection), were not available or because the landscape surrounding a route had undergone major structural change (e.g. forest cutting, urban development) sometime during the study period. The final pool used in analyses consisted of 200 routes located in Arkansas, Kansas, Louisiana, Missouri, Oklahoma, and Texas (Fig. 1).

Landscape Sampling

Landscape structure was measured using digital land-cover maps of the area surrounding each BBS route. For each map, we classified the occurrence of six different land-cover types within a 1-km band on either side of a route. While some birds observed during surveys may have nested outside of the landscape-sample area, we assumed that measures of landscape structure were reasonable estimates of the landscape near, but outside of, this area. Land-cover types used in the classification

were: (1) urban, (2) closed forest (< 1 canopy width between trees), (3) open forest (> 1 and < 20 canopy widths between trees), (4) open country (> 20 canopy widths between trees), (5) water, and (6) bare ground. These types followed those developed by Anderson (1976; Level I) with some modifications. Patches of different land-cover types were classified by visual interpretation and digitized from 1:40000 National High Altitude Photography (NHAP) panchromatic aerial photographs taken from 1989 to 1991. Photography was obtained from the U. S. Farm Service Agency, Salt Lake City, Utah (formerly the Agricultural Stabilization and Conservation Service). Vector-format maps of land-cover patches were created using the Geographic Resources Analysis Support System (GRASS ver 4.1; CERL 1989) and then transformed into 100-m-resolution raster-format maps prior to analysis.

Landscape measures were calculated using the r.le sub-program (Baker and Cai 1992). Landscape variables measured for each route included: (1-3) percent open country, open forest, closed forest; (4-6) mean patch size open country, open forest, closed forest; (7-9) number of open-country, open-forest, closed-forest patches; and (10) sum of the length of edge between open country and open forest, open country and closed forest , and open forest and closed forest (Table 1).

Percent coverage of open country and open forest were used as one estimate of nesting-habitat fragmentation, consistent with the use of percent forest cover in studies of the effects of fragmentation on forest-dwelling birds (e.g. Andren 1992, Donovan et al. 1995, Robinson et al. 1995). We evaluated fragmentation of both of these habitat types because scissor-tailed flycatchers use both for nesting and foraging (Fitch 1950,

Regosin and Pruett-Jones 1995, Nolte and Fulbright 1996, Certain 2000), and because the percent coverage of these habitats in the landscape are important to nest-site selection (Certain 2000). Fragmentation of closed forest may be important because forest fragmentation is often associated with an increase in forest-edge habitat which serves as a source for many potential nest predators (e.g. birds, mammals, snakes) on scissor-tailed flycatchers. Percent-cover variables were measured as the ratio of the number of pixels (1 pixel = 1.0 ha) of a land-cover type within each sample area to the total number of pixels.

We also measured the number of open-country and open-forest habitat patches as an alternative estimate of nesting-habitat fragmentation. Percent coverage alone provides little information about the spatial distribution of a given habitat type, i.e. smaller percent-coverage values are not necessarily related to a fragmented and patchy distribution. The number of open-country and the number of open-forest patches were both positively associated with woody edge length in the environment.

We tested for the effects of mean patch size of open-country habitat because scissor-tailed flycatchers have been shown to preferentially select nest sites in large, open patches that are isolated from woody edges (Certain 2000). Mean patch size of open-forest and closed-forest habitats may be important since both serve as sources for potential nest predators.

Our measure of the total length of woody edge was used to estimate physical characteristics of edges in the landscape. Newly created edge environments may act as "ecological traps" (Gates and Gysel 1978), attracting nesting birds that may not have

appropriate nest defense strategies for areas with a high diversity and abundance of potential nest predators. While the many studies of edge effects in forested landscapes continue to generate debate about their importance to avian productivity, there have been relatively few investigations into how edges influence species nesting in open habitats outside of woody patches (Johnson and Temple 1986, Møller 1989, Vickery et al. 1992, Burger et al. 1994, Certain 2000, Winter et al. 2000). In the current study, total-edge length was calculated by first summing the number of times open-country and closed-forest, open-country and open-forest, and closed-forest and open-forest pixels shared a common pixel edge. This value was then multiplied by the length of a pixel edge (100 m). The shared corner of two pixels (diagonal adjacency) was not counted as an edge.

Statistical Analysis

All variables were transformed prior to analysis to better meet assumptions of parametric tests (see Table 1). Associations among landscape variables were first evaluated using Pearson product-moment correlations with Bonferroni adjustments for multiple tests (Sokal and Rohlf 1995). Because of strong correlations among variables, we developed a new set of uncorrelated variables using principal components analysis (PCA). Major trends in the original variables were represented on principal components calculated from a correlation matrix produced using standardized data (variable means of 0.0 and standard deviations of 1.0). We kept all resulting principal components with

eigenvalues equal to or greater than 1.0. Component scores were based on standardized data and were used as input values for subsequent analyses.

Stepwise linear multiple regression was used to estimate the model that best fit the relationship between the new composite variables and log-transformed (ln) mean abundance. In multiple regression the dependent variable is modeled using two or more independent variables. The stepwise method uses specific statistical criteria to determine which variables enter into the model and which are removed. The *F*-to-enter in the regression function was set to 4.0, while the *F*-to-remove was 3.9.

We used Mantel's test (Mantel 1967, Manly 1997) to examine the overall spatial pattern in relative abundance of the scissor-tailed flycatcher and in each of the composite landscape variables. The simple Mantel test (Mantel 1967) measures the correlation between two symmetric distance matrices. Each distance matrix in our analysis consisted of the euclidean distance between all pairs of sites for each variable. The significance of the matrix correlation is determined by iteratively randomizing one of the matrices and recalculating the correlation coefficient between matrix elements. The *P*-value is equal to the number of times that the correlation coefficient, using the randomized matrix, is equal to or exceeds that for the original matrices. We employed this test using 1000 iterations to determine if closer routes were more alike than distant routes (spatially autocorrelated) for each variable.

Mantel's test has also been modified to accommodate more than two distance matrices (partial Mantel; Smouse et al. 1986, Manly 1997) by using multiple regression to estimate the effects of two or more independent variables on the dependent variable.

We used this technique to statistically control for the effect of geographic distance while examining the association of each composite variable with relative abundance. The regression model that estimated change in mean abundance against all independent variables was:

$$A_{ij} = a + b_{A|E.S}\, E_{ij} + b_{A.S|E}\, S_{ij} + \in_{ij},$$

where A_{ij} is the difference in mean abundance between sites i and j; a is the intercept of the regression line; the beta coefficient, such as $b_{A|E.S}$, denotes the relationship between A and an independent variable (e.g. E; environmental distance) while allowing for another independent variable (e.g. S; geographic distance); $\in_{ij}$ is an independent error term. Significant associations between differences in components and differences in abundance, after factoring out spatial structure, would suggest that spatial autocorrelation was not the driving factor behind these associations.

Results

Principal components

The first three components from the principal components analysis had eigenvalues greater than 1.0 and explained 89.3% of the total variance among the 10 landscape variables. Components were interpreted as describing one or more characteristics of

sample areas based on the relative correlations of components with original variables (Table 1). Loadings (i.e., correlations of components with original variables; Table 1) and projections of standardized scores on component axes (Figs. 2A,B) indicated that component I represented a gradient from routes with a relatively high percent cover and large mean patch size of open country to routes with a high number of open-country patches, a high percent cover and large mean patch size of closed forest, and a long woody edge length. Component II represented a gradient of routes with an increasing percent cover and mean patch size of open forest. The loadings and projections on component III (Table 1, Fig. 2B) reflected a gradient of routes with an increasing number of closed-forest and open-forest patches. Routes with the largest number of patches were considered to be the most fragmented.

Standardized scores were also projected (Figs. 2C,D) using labels of class values that reflected the mean abundance of scissor-tailed flycatchers at each route during the study period. This was done to examine the distribution of routes that vary in mean abundance along component axes. Class values used to label route projections were as follows: (0) 0.0; (1) 0.1 - 20.0; (2) 20.1 - 50.0; (3) 50.1 - 70.0; (4) 70.1 - 100.0; and (5) 100.1 - 120.0. Routes in the two highest abundance classes (4 and 5; 70.1 - 120.0) all had positive component-II scores (Fig. 2C) while 20 of 26 routes with no scissor-tailed flycatchers observed (Class 0) had negative component-II scores. This suggests an association of the highest-abundance routes with relatively high percent cover and large patch size of open-forest habitat. Routes where scissor-tailed flycatchers were not observed during the study period tended to have a relatively low percent cover and small

patch size of open-forest habitat.

Linear regression

Results of simple linear regression of log-transformed mean abundance on each component (I-III) are shown in Fig. 3A-C. Components II (Fig. 3B) and III (Fig. 3C) both showed a significant, positive association with abundance. Components II (F-to-enter = 34.4) and III (F-to-enter = 15.4) entered into the multiple regression model and together explained 21% of the total variance in abundance ($F = 26.13$, $P < 0.001$). Theresultant regression model that described the relationship between log(mean abundance) (Y) and components II (X_{II}) and III (X_{III}) was as follows:

$$Y = 0.713 + 0.612\, X_{II} + 0.509\, X_{III}.$$

Spatial analysis

Plots of component scores showed variation in the spatial pattern of distribution across the range of the scissor-tailed flycatcher (Fig. 1B-D). The distribution of scores also differed in their relationships with the spatial distribution of mean abundance in the scissor-tailed flycatcher (Fig. 1A). Component I exhibited a gradient from routes with more open country in the west to those with more closed forest in the east (Fig. 1B). This gradient is associated with the transition from grassland to cross-timbers to eastern deciduous forest moving from west to east across the range of the scissor-tailed

flycatcher. The highest scores for routes on component II were all located in the southwestern portion of the distribution (Fig. 1C) and these represented sites with the highest amounts of open forest. High scores on component III represented routes with a relatively large number of open-forest and closed-forest patches. These are routes associated with the greatest degree of fragmentation, both natural (e.g. cross-timbers) and human-induced, and generally occurred as a swath of routes running north and south through the central portion of the scissor-tailed flycatcher's range (Fig. 1D).

Results of Mantel tests showed that there was large-scale spatial autocorrelation in mean abundance, component I, and component II (Table 2, Fig. 4A-C). Spatial structure contributed to the strength of associations between these two composite variables and mean abundance, but each exhibited a significant ($P < 0.05$) association with mean abundance even after allowing for autocorrelation (Table 2). Mean abundance was not significantly associated with component III, even after accounting for autocorrelation in abundance.

Discussion

The relative abundance of scissor-tailed flycatcher's was significantly associated with composite measures of landscape structure even after accounting for the spatial autocorrelation of these variables. Results of this analysis are consistent with previous

findings that Neotropical migrants as a group were associated with measures of landscape structure including amount of edge, habitat patch number, and habitat patch size (Flather and Sauer 1996). Our analysis further demonstrates that associations of landscape structure and composition with relative abundance exist at the scale of the geographic range of a species and not just within a portion of its' range.

The positive regression relationship with component III suggests that scissor-tailed flycatcher abundance is partially explained by an increase in landscape fragmentation. This result may, in part, be explained by the evolutionary history of the scissor-tailed flycatcher that nests and feeds in naturally fragmented habitats throughout much of it's breeding range. Examination of the spatial distribution of component III scores (Fig. 1D) shows that many routes with relatively high scores (i.e. large number of open- and closed-forest patches) are located in the eastern portion of its' range where cutting of once contiguous forest has increased the number of open patches now available for colonization by scissor-tailed flycatchers.

Spatial structure is often a feature of ecological datasets at a wide variety of scales, and can be used to investigate the relative importance of ecological processes in particular systems. The presence or absence of autocorrelation in the annual abundance of bird populations has been used to investigate the role of metapopulation processes in determining local abundance over a large area (Koenig 1998). Koenig (1998) found that California migrant-songbird populations were more highly spatially autocorrelated from year to year than resident or short-distance-migrant birds and suggested that this was the result of migrants being less subject to metapopulation processes and more greatly

influenced by patterns of natal dispersal. Alternatively, autocorrelation may result from strong gradients in biotic and abiotic factors that influence local reproductive success (e.g. moisture, temperature, predation, nest parasitism). While our dataset does not address synchrony in year-to-year abundance, our results do suggest the importance of factors, other than dispersal, in determining local population abundance.

Acknowledgements We are grateful to Linda Bird, Chuck Dillon, Raniyah Ramadan, Jane Sund, John Ware, and Brad Watkins for the many hours spent digitizing aerial photography. We also thank Dan Hough for his assistance with computer issues. Financial support for this work was provided by: U.S. Department of Defense, U.S. Army Research Office, and Office of Naval Research (AASERT No. DAAH04-93-G-0093); Department of Zoology, University of Oklahoma; Oklahoma Biological Survey; and George Miksch Sutton Scholarships in Ornithology. We appreciate the comments of Mark V. Lomolino, William J. Matthews, Caryn C. Vaughn, and T. H. Lee Williams on earlier versions of this manuscript.

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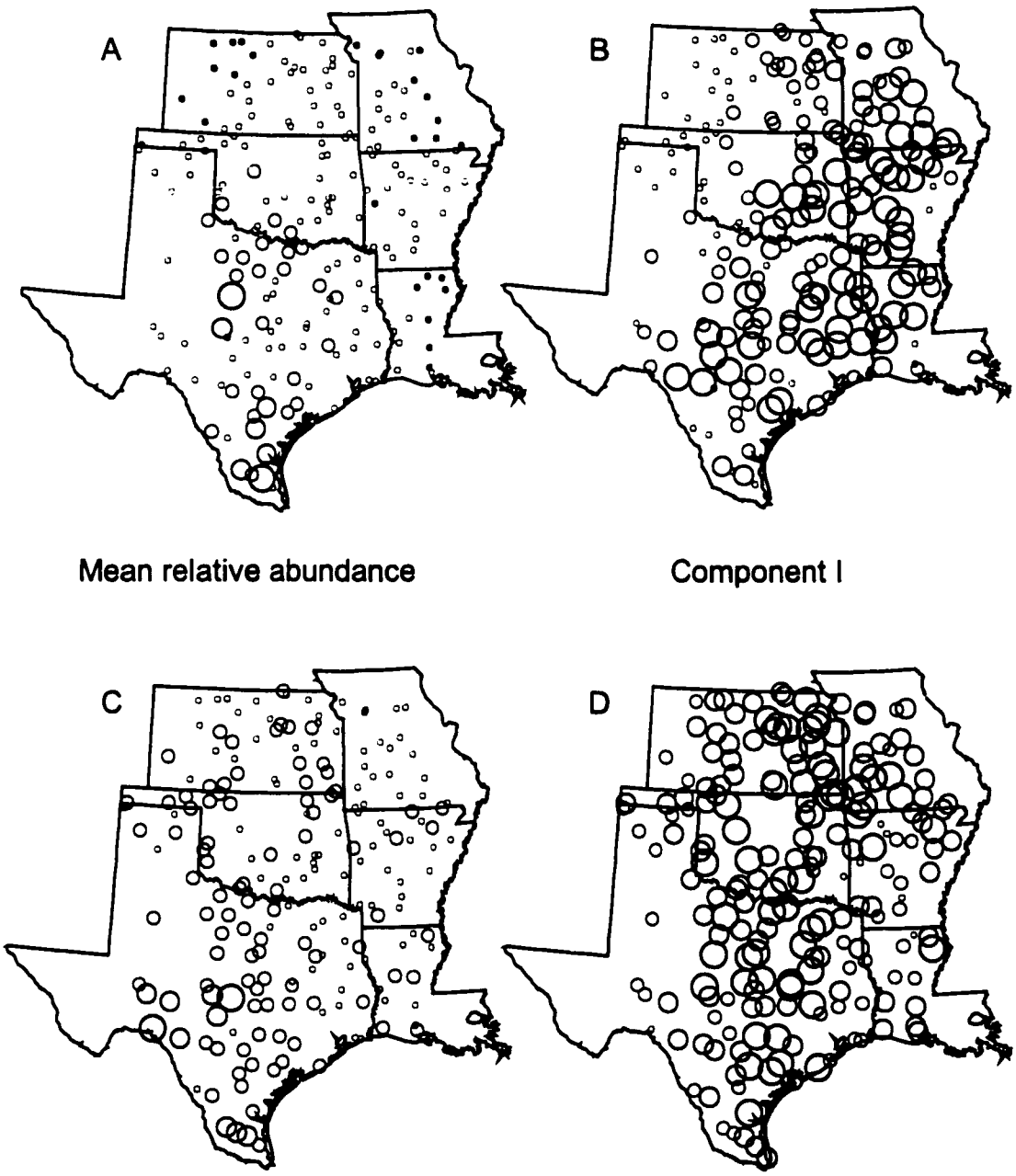
Fig. 1 Geographic distribution of mean relative abundance of scissor-tailed flycatchers (A) and standardized principal-component scores (B-D). Black circles in panel A represent routes where no scissor-tailed flycatchers were observed. Size of open circles increases with relative value of variable. Total number of points (routes) in each map is 200.

Fig. 2 Projections of standardized component scores for BBS routes onto principal components I, II, and III resulting from analysis of 10 landscape-structure variables. Panels C and D are identical projections of panels A and B, but with abundance-class values used as labels. See text for detailed description of class values.

Fig. 3 Plots of log-transformed (ln) mean abundance values against components I, II, and III with linear-regression lines fitted to distribution.

Fig. 4 Plots of geographic distance against differences in mean abundance and components I, II, and III. Size of plotting symbols indicates relative number of points, with smallest circles indicating single point and largest indicating up to the following number of points: (A) 400; (B) 800; (C) 400; (D) 600. Total number of points in each graph is 19,900.

FIG. 1



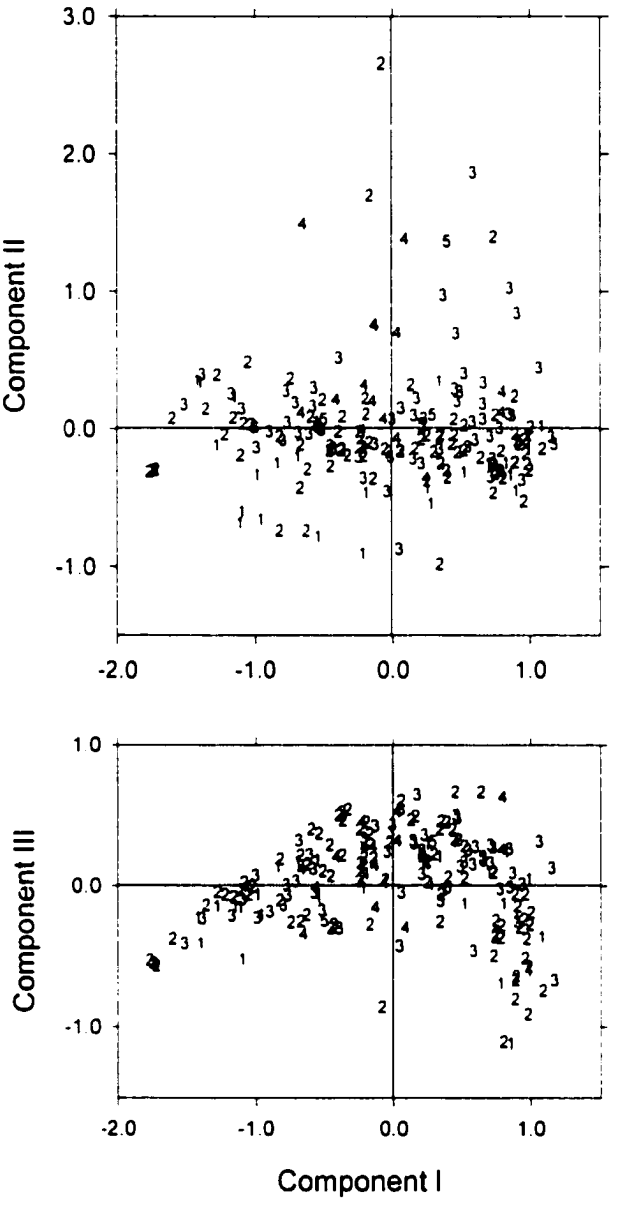
Mean relative abundance

Component I

Component II

Component III

FIG. 2


3.0
2.0
1.0
0.0
-1.0
Component II
-2.0
-1.0
0.0
1.0
1.0
0.0
-1.0
Component III
-2.0
-1.0
0.0
1.0
Component I

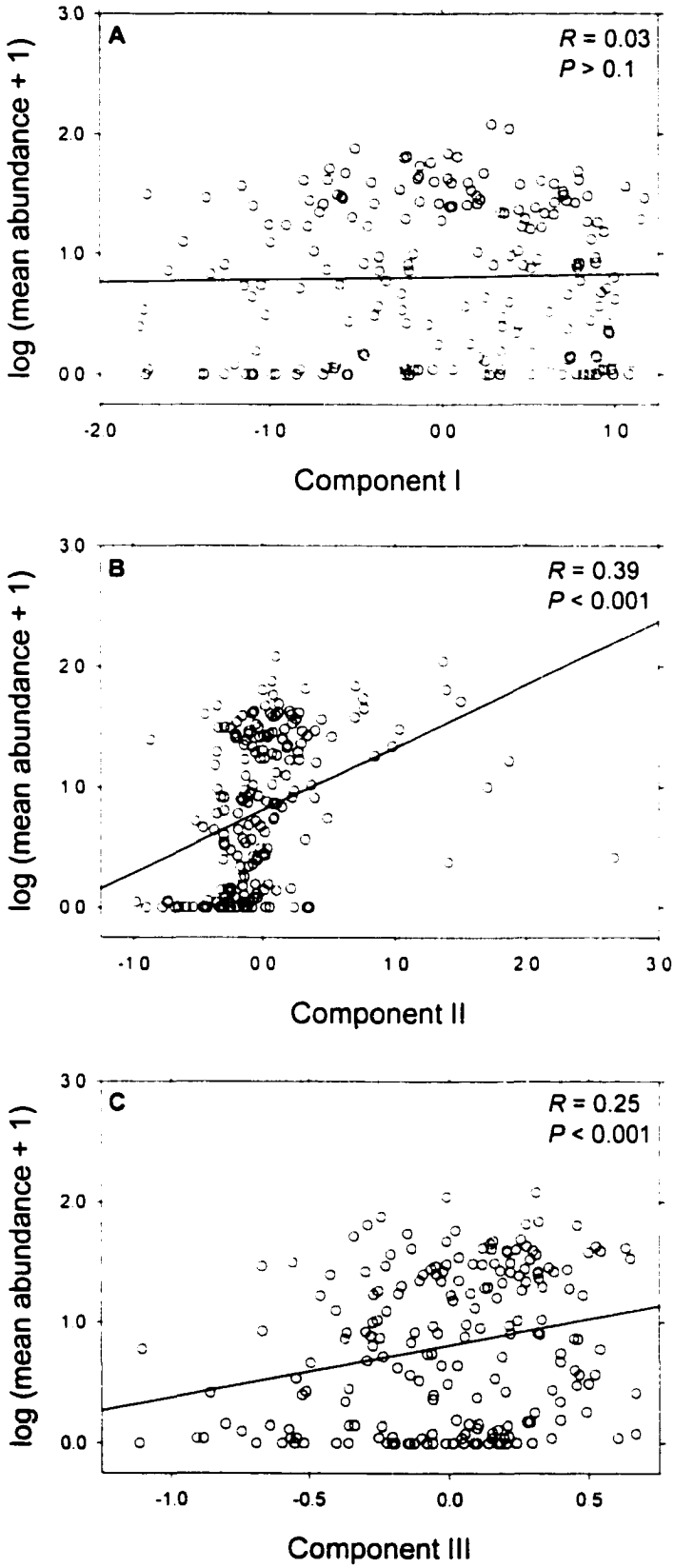

A
R = 0.03
P > 0.1
log (mean abundance + 1)
Component I
B
R = 0.39
P < 0.001
log (mean abundance + 1)
Component II
C
R = 0.25
P < 0.001
log (mean abundance + 1)
Component III

FIG. 3

FIG. 4

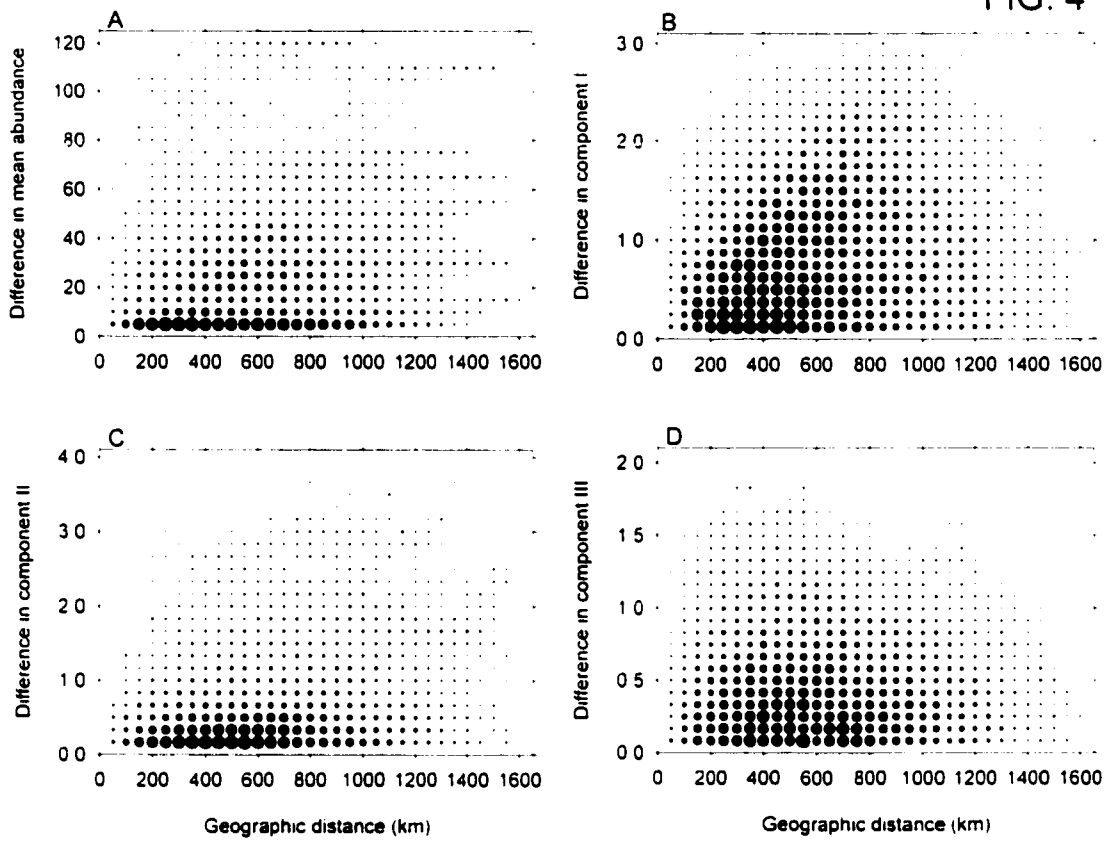

A
B
C
D
Difference in mean abundance
Difference in component I
Difference in component II
Difference in component III
Geographic distance (km)
Geographic distance (km)
0
200
400
600
800
1000
1200
1400
1600

Table 1 Loadings, eigenvalue, and percent variance explained from principal-components analysis based on landscape variables[a]

Variable	Component I	Component II	Component III
1. Percent open country[b]	**-0.90**	-0.18	0.34
2. Percent open forest[b]	0.31	**0.90**	0.05
3. Percent closed forest[b]	**0.88**	-0.33	-0.28
4. Open-country patch size[c]	**-0.95**	-0.08	0.22
5. Open-forest patch size[c]	0.30	**0.89**	0.05
6. Closed-forest patch size[c]	**0.82**	-0.27	-0.28
7. No. open-country patches[c]	**0.95**	-0.07	-0.04
8. No. open-forest patches[c]	0.60	0.28	**0.53**
9. No. closed-forest patches[c]	0.50	-0.36	**0.71**
10. Woody edge length[b]	**0.86**	-0.21	0.37
Eigenvalue	5.61	2.08	1.25
Variance explained (%)	56.09	20.76	12.48

[a] Relatively high absolute loadings (component I, |0.8|; II, |0.8)|; III, |0.5|) in bold

[b] Variables arcsin transformed prior to analysis

[c] Variables log (ln) transformed prior to analysis

Table 2 Results from distance-matrix comparisons between abundance and geographic location (space) and between abundance and principal component matrices (t_A), and between space and principal component matrices (t_S). Last column ($t_{A.S}$) shows results of Mantel tests between abundance and principal component matrices after accounting for spatial structure. Significant values ($P < 0.05$) in *bold type*

Variable	t_A	t_S	$t_{A.S}$
Component I	**-11.65**	**29.35**	**-19.99**
Component II	**25.77**	**35.86**	**17.93**
Component III	-4.86	-0.33	-4.93
Space	**36.26**		